THE

STRUCTURE AND FUNCTIONS

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BRAIN AND SPINAL CORD.

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Being the Fullerian Lectures for 1891.

BY

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WITH NUMEROUS ILLUSTRATIONS.

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PREFACE.

The following Lectures, which are published at the request of some of those who heard them at the Royal Institution in 1891, have no pretensions to form a monograph upon the subject of which they treat. They are merely an elementary review of it, based upon modern physiological and anatomical research. It is intended that the present volume, which discusses the spinal cord and ganglia alone, shall be followed by two others—the subsequent courses of the Fullerian Lectures—one of which has been already delivered, and the other, it is hoped, will be given in the coming year. These deal with the structure and functions of the great brain, or cerebrum, and the little brain, or cerebellum. In the last course, some of the recent results of research in Physiological Psychology will be described.

In illustration of the present volume I am very greatly indebted to the kindness of Professors Cienkowski, Ecker, Eimer, Gad, Hæckel, His, Kleinenberg, Kölliker, Retzius, and Romanes, for the permission to use drawings from their original papers.

Several figures have also been borrowed, by kind permission, from Professors Landois and Stirling's *Text-book of Human Physiology* and other sources.

Finally, the tedious work of correcting the proof-sheets and of compiling an index has been undertaken by my wife, whose unfailing judgment and criticism I cannot sufficiently acknowledge.

V. H.

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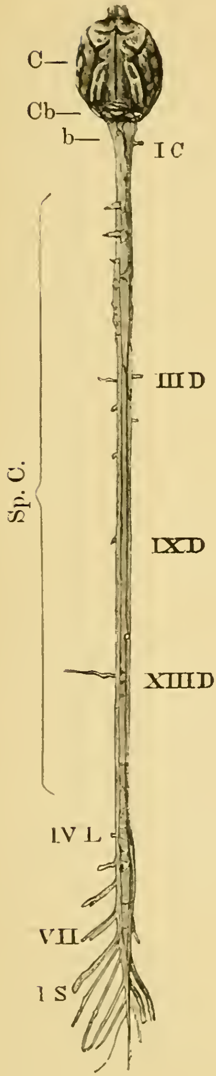
GENERAL CONTENTS.

LECTURE I.

The study of the central nervous system, of its structure and functions, is interesting and important to every one, and not necessarily only to specialists, such as neurologists, anatomists, and physiologists. But although it is easy to construct in our minds the general outline of the nervous system, such as we see it exemplified in the higher animals, it is nevertheless impossible to connect our popular preconceptions of its function with the actual facts, as they are now being rapidly accumulated by modern research, unless we first pass in some sort of review, however brief, the growth and development of the ideas on this subject, many of which have often suffered change only after centuries had familiarised them into household words, if not household truths.

A good example of the object of our study is shown in Fig. 1—viz., the central nervous apparatus as it exists in the cat: the main parts of which are

FIG. I.



familiar to all of us—the large brain or cerebrum (C), the small brain or cerebellum (Cb), and, in intimate connection with both of these, the spinal cord or marrow (Sp. C), the upper part of which is designated the medulla oblongata or bulb (b). In intimate relation with the spinal cord, observe some of the numerous spinal nerves which arise by two roots—one motor, one sensory—and are distributed to the various parts of the body.

One small point of detail I must not omit from this outline, on account of the extraordinary prominence which was given to it by the ancients—I mean the relatively unimportant fact that the central nervous system, and specially the cerebrum, is tunnelled by a small cavity, which, widening somewhat above in the large brain, is there termed the

lateral ventricle. It is well shown (LV) in this photograph (Fig. 2) of a transverse section of the whole head, giving you its true proportions.

Turning now to the subject of the present lecture,

FIG. 2.

The skull is sawn across with the brain *in situ*.—*Key and Retzius.*

c.c.=Corpus callosum.
LV=Lateral ventricle.
c=Caudate nucleus } Corpus striatum.
str=Lenticular nucleus } Corpus striatum.
na=Amygdaloid nucleus.
p=Pituitary body.
B=Base of skull (basi-sphenoid).

we shall be astonished to find that the ancients were but very imperfectly acquainted with the brain and spinal cord, and that it was not until many years after the foundation of Greek psychology

that they became aware even of the existence of nerves, or, as we now prefer to call them collectively, the peripheral nervous system. Beginning therefore with Plato, who has reflected for us the first genuine crystallisation of thought upon that combination of structure and function which we call "neurology," we learn at once the intimate relationship which popular beliefs and earliest traditions have borne to what is commonly known as "psychology." Thus we find that he starts by imagining that the Deity formed sublunary beings in part of His own nature, and that to these the duty of the manufacture of animal bodies was entrusted. In man, accordingly, an immortal part, of the same nature as these sublunary beings, was supplied with a body, a material structure. The soul consisted, according to this view, of two, or, to speak more properly, three parts, which were (1) the spiritual, the intelligence; (2) the material, which included, first of all, anger or courage, or the passionate element; and, secondly, the lower appetites. And here we have clearly shown the popular distinction between purely mental phenomena and those (other) mental phenomena which are more easily recognised as belonging to the physical life. The next step was to apply this view of human psychology to the bodily system as then known. This was achieved as follows:—The sphere

being considered by the ancients as the symbol of perfection, Plato regarded the more or less globular head as the seat of the intelligence and of perception; while as to the more material phenomena, he placed the passionate element in the heart (arguing imperfectly from the changes in the action of that organ under the influence of passion), while the bodily desires he assigned to the lower parts. This psychology was greatly confused by many elaborate corollaries which were built upon it as a result of discussion apart from direct observation.

Hippocrates and his pupils, following in the same line, became led into a number of hypothetical considerations, which involved them in such extraordinary errors of fact as to render it impossible for us to profitably pursue their lines of thought.

Even Aristotle, who at the close of the fourth century B.C. was provided by Alexander with a splendid laboratory, furnished with specimens gathered from all parts of the world at practically any cost, although pursuing truly scientific investigation, was led into similar pitfalls by theorizing from incomplete observations. Aristotle's laboratory research has been to a large extent preserved to us—the first great example of the results of State aid to science; but, unfortunately, what would have

been the most interesting relic has disappeared. I refer to the anatomical drawings which he is known to have had constructed by many artists. His system of psychology, which is divisible into the headings of imagination, judgment, and sensation, soon became inapplicable, in the progress of anatomical knowledge, to the actually observed structure of the nervous system. And indeed, when we examine his views in detail, we find that he did not really discover the nerves as separate tissues or as having special functions; and in fact, having been led from theoretical reasons to consider the brain as merely an instrument for cooling the heart, he was obliged to regard this latter as the seat of the soul, or as we would say nowadays, perhaps, the mind. Hence it was not until some years after, that solid progress in the investigation of our subject was attained by the only legitimate method—viz., direct scientific observation and experiment—carried out especially by Herophilus of Alexandria, who about 300 B.C. occupied the chief position in the extensive laboratory, erected by Ptolemy I. in a large building which included the well-known and splendid Library and Museum, built among the palaces in the Bruchium or royal quarter of Alexandria. By means of his human dissections he was the first to discover the peripheral nervous system or nerves, that these

latter were connected with the brain and spinal cord, and that they conveyed sensory impressions. After him another investigator, whose influence was very great—I mean Erasistratus—either invented or concentrated prevailing ideas respecting the relation between the nervous system as a structure, and mental phenomena as its function, which ideas, although absurdly erroneous, nevertheless held their own for something like 1500 years, and were based upon the destination of the air which we inhale into the lungs. Erasistratus thought that this air underwent a kind of elaboration in the lungs, that thus altered it passed to the heart, where it again underwent change, and from the heart travelled to the brain, where in the ventricles it became converted into animal "spirit." Now this animal "spirit," or "vital spirit," which I now refer to for the first time, is a most interesting fact as regards the development of knowledge of the function of the nervous system, for it represents the first glimmerings of the truth that, what we call, mental phenomena are the concomitants, if not the results, of the functional activity of the brain and spinal cord, and is also the first attempt to refer those phenomena to their undoubted source. This work of Erasistratus, although popularising vague and illogical views, nevertheless received

complete and scientific examination at the hands of the great Roman physician, Galen.

Galen, who was of Oriental origin, appears to have been a man like Hunter of modern time, in that he was capable of regarding such a great subject as that which we are now examining with a remarkable breadth of view, considering the uncertainty of general knowledge in his day. Educated, of course, at Alexandria and Pergamos, his ideas on the nervous system reflect the best and latest teaching of those great schools; but the immense advance which his writings show is evidently due for the most part to his own genius, an example of which I should like at once to quote. I have just reminded you of the origin of the theory of the animal spirit, or pneuma. Galen, while he accepted the existence of this pneuma, showed by the direct experiment of opening an artery in an animal that it was not the one thing of importance in the vascular system (as Erasistratus supposed), but that the blood-vessels contained blood, and that probably the pneuma, or spirit, was mixed with the blood. Upon this last point he gives remarkable evidence of his scientific mind by stating that he has no proof—*i.e.*, experimental—of the existence of the pneuma, saying, in fact, that he only regards it as a means of explaining problems otherwise inexplicable, and in this respect his use of the

expression is exactly parallel to that of the term "ether" by modern physicists. Following no doubt his teachers, but improving on their ideas, he believed that the brain was the chief of the nervous structures, and was the seat of all sensation and voluntary movement, and by his great anatomical industry he discovered the more important of the innumerable details in the structure of the brain, nerves, and muscles. But the extraordinary strength of Galen's position, and the remarkable force of his writings, many of which are fortunately preserved to us, depend upon the fact that he clearly recognised the body to be a physical structure, and consequently that its functions could only be truly determined by the physical method of experiment, and it was by the employment of this method that he discovered not only the fundamental facts of the circulation and of the respiration, &c., but determined, by devising the following experiment, that the nerves were the source of muscular contraction. As we shall see in our subsequent study of comparative neurology, this discovery by Galen of the foundation of neuro-muscular physiology has been the key to all subsequent discovery from his epoch—viz., from that of the Emperor Commodus—to the present year. The experiment by which he revealed this fact was, like most great scientific advances, a very simple one. He divided in an

animal the fifth spinal *nerve* in the region of the neck, and found as a consequence that all movement was lost in the *muscles* of the shoulder which were supplied by that nerve. I could multiply largely the wealth of knowledge obtained by Galen's observations, but time will not permit more than another example, in which he shows the folly of reasoning without experiment. I refer to Aristotle's great theory that the brain cooled the heart. Galen, by simply exposing the brain in an animal, discovered that it was as hot as the heart.

In the chaos which followed the fall of the Roman Empire, and in the unusual transmigrations of peoples which accompanied that general disintegration of the then civilised world, we are quite prepared to learn that, like all other forms of knowledge, scientific investigation practically ceased, and, indeed, only received cultivation again after a powerful race had once more succeeded in constituting itself out of the general ruin. This, relatively speaking, was first accomplished by the Arabs. As soon, therefore, as we find them settled in their new metropolis at Bagdad, we learn that a College of Medicine was instituted by the Khalifs; and when the Saracenic dominion was carried into Spain, a similar development of knowledge was obtained by the institution of splendid libraries and schools at

Cordova and Seville. Here, unfortunately, with all this great wealth of educational appliances, the religious dogmas of this singular people prevented their achieving as wonderful a progress in neurology as they attained in chemistry. For, believing as they did, that the soul only left the body very slowly after death, the dissection of human beings involved too great risk of torture to the dead person to permit of such a practice becoming general, and for this, among other reasons, was considered incompatible with Islamism. Consequently, up to the tenth century we find that the great Arabian physicians, who added vastly to our knowledge of drugs and empirical treatment of disease, were nevertheless reduced to furbishing up the old Greek views of neurology, which they obtained principally by translations, made by their Syrian slaves, of the manuscripts which fell into their hands upon their conquest of Alexandria and other Greek cities.

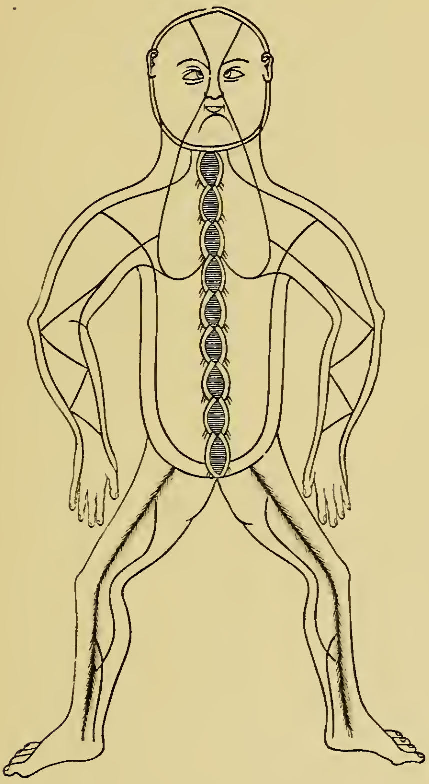
In this way we are brought, without any tangible progress in the knowledge of our present subject, from Galen's time into the mediæval epoch, which we may take as beginning with the tenth and eleventh centuries; but it is an interesting confirmation of the general advance made by the Arabs in other branches of learning, that when we investigate the circumstances under which knowledge of any kind,

but especially science, was brought into mediæval England, at the time of the Conquest, we find, that the English monks or students who travelled abroad for the purpose, went to the south to the Arab Universities, as well as to Athens. Thus the introduction of Greek science and philosophy was achieved by John Basyng, a student of Oxford, in the eleventh century, who travelled as far as Athens, and thence brought back the MSS. of the Greek authors ; while a Benedictine monk, of Bath, named Abelard, travelled among the Spanish Moors, and spent many years in Spain, translating both Greek and Arabian MSS., which he subsequently brought to England. Such monks also produced compilations from the Greek MSS., one of the earliest of which, obviously based upon the psychology of Aristotle, is to be found both in the Cottonian and Ashmolean collections on Human Physiognomy. It was apparently written in the year 1152, and, bound up with the Oxford copy, is, for us, a still more interesting MS. of the same epoch on the structure of the human body, and infinitely precious to us since it is illustrated by drawings. Through the courtesy of Mr. Nicholson, the Bodleian Librarian, and of Mr. Hart, the Controller of the Clarendon Press, I am enabled to show in Fig. 3 an outline from a photograph* of the

* Kindly verified for me by J. Fairbairn, Esq.

drawing which illustrates the nervous system in this valuable work. It is easy to see that, as

FIG. 3.



a matter of fact, it does not take us one step beyond the ideas of Aristotle, and Galen's teaching is almost ignored. That is to say, hundreds of years had passed by without the difficult problem of the nervous system receiving practically any further

solution. Notice that in the figure, the brain is not even indicated, a significant proof of the contempt in which Aristotle held it as being merely a cooling apparatus; but notice also that the artist has carefully drawn a pair of nerves arising on each side from the central cords, the correctness of which, of course, was due to Galen.

At the close of the twelfth and the beginning of the thirteenth century, the Church of Rome became apprehensive of the results of the introduction of Greek philosophy and science, and in Paris Aristotle's works were publicly burned, and the students who read him were persecuted; in a short time, however, the desire for truth reasserted itself, and the Governments of the various countries gradually supported the dissemination of learning, and enlarged the foundations of the Universities.

With the Renaissance of general literature in Italy, there began that remarkable development of physical science in that country which culminated in such a brilliant aggregation of scientific knowledge. The study of anatomy became a recognised branch of education, and with the lectures by Mondini, who was Professor in Bologna in 1315, we find a combination of mediæval anatomical research and Arabian therapeutics. Shortly after, all the Universities followed this example, and provided that a

body should be annually dissected, though it is rather astonishing to find that, until the next century, this was usually performed by a barber's assistant with a razor. In the fifteenth century, anatomical research was immensely extended in Italy, and formed the foundation upon which in England two great physiologists, Harvey and Willis, succeeded in the seventeenth century, in erecting their structures of the circulation and nervous system respectively, which effected a complete revolution in each of those subjects; their epoch consequently, after the troubles of the Commonwealth, forms a fresh level of knowledge which has undergone extension rather than modification during the two centuries which have subsequently elapsed. It is now only 206 years since Willis's researches on the central nervous system were published in his native language, and they exhibit such an extraordinary grasp of the function (and its corresponding relation to structure) of the brain and nervous system generally, that I shall give verbatim some of his statements, for they deserve far more than a passing summary, inasmuch as it will be seen, as these lectures proceed, that his remarks are almost invariably logical and accurate deductions from the actual facts which he observed. In the first place, we may note the way in which he completely throws over the teachings

of the Greek and Roman schools, which fell into the very natural but profound mistake of regarding the peripheral phenomena in the heart as the index of local psychical changes, instead of mere secondary indications of central ones. For he states that the brain is "the chief seat of the rational soul in a man and of the sensitive in brute beasts; and indeed, as the chief mover in the animal machine, it is the origin and fountain of all motions and conceptions." But the next point of vital importance which he first clearly enunciated was that which occupies the attention of all neurologists at the present time, and which is probably the greatest advance gained in psychology ever since it became a science—I mean the localisation of function to distinct parts of the nervous system. The first place where he shows us that localisation of function must exist is when he is attempting to explain the reason why the cortex or surface of the brain is thrown into convolutions, or "cranklings" as he calls them. Upon this point he speaks as follows: "For as the animal spirits for the various acts of imagination and memory ought to be moved with certain and distinct limits or bounded places, and those motions to be often iterated or repeated through the same tracts or paths, for that reason these manifold convolutions and infoldings of the brain are required for these divers manners of

ordinations of the animal spirits—to wit, that in these cells or storehouses severally placed might be kept the species of sensitive things, and as occasion serves may be taken from thence."

He subsequently developed this theory, and showed that the cortex or surface of the brain, was, as we now know it truly to be, the seat of origin of the ideas, and further that (page 106) its excitation, which he represented as spirits, passed from the cortex into the substance of the brain, and thence into the spinal cord and nerves. The passage of the nerve impulses along the nerves, or, as we now know them, along the nerve fibres, is a point of such vast importance that I may be permitted here to digress a little for its discussion; the more especially as Willis, by reason of the imperfect means of anatomical research, fell into an error, which itself actually becomes invested with the greatest interest when we discover, as we shall directly, that it was not shared by Willis's great contemporary, Sir Isaac Newton, although the latter was not a physiologist. Thus Willis says that the nerves themselves, as may be discovered by the help of "a microcosm or perspective glass, are furnished throughout with the cords and passages, as it were so many little holes in a honeycomb." And he goes on to compare the

nerve to a porous cane. The passage of the nerve impulses he describes as follows: "Within these little spaces the animal spirits or very subtle little bodies, and of their own nature ever in a readiness for motion, do gently flow." And he subsequently goes on to suggest that the cerebral spinal fluid which bathes the brain and the spinal cord goes with the spirits, thus: "This nervous juyce being derived from the brain and cerebel into the medulla appendix, is carried from thence by a gentle sliding down through the nerves." Now here we see how so great a man as Willis was influenced by general beliefs prevailing on the subject of the soul, &c., whereas the unbiassed mind of Newton, proceeding at the same epoch of time from the very definite facts of experimental physics, forestalled the views concerning the nature of nerve impulses and their passage along nerve fibres which are current at the present day—*i.e.*, about 200 years after he wrote. For among the celebrated questions which are to be found at the end of his "Optics," he says: "Qu. 12. Do not the rays of light in falling upon the bottom of the eye excite vibrations in the tunica retina, which vibrations, being propagated along the solid fibres of the optic nerves into the brain, cause the sense of seeing?" And he goes on to show why it must be the solid part of the nerve which thus conducts.

But now, leaving this point, I wish to make one more remark concerning Willis's great improvement in our knowledge of the workings of the brain or cerebrum. I have shown you how even Galen fell in with the views of the later Greeks, and believed that the ventricle of the brain had a great deal to do with the activity, if not the manufacture, of the animal spirit—*i.e.*, the nerve energy. As Willis says: "The ancients have so magnified this cavern that they affirmed it the shop of the animal spirits, both where they themselves were appropriated and performed the chief works of the animal functions." And then he goes on to say that this is absurd, that the animal spirits are such volatile little bodies that they would fly away out of the cavity; and it is very amusing to read his more or less contemptuous introduction of us to the true function and object of this cavity, for he shows that it is usually full of fluid, adding, "Wherefore almost all anatomists who are of a later age"—observe the word "later"—"have attributed a vile office of a jakes or sink to this more inward chamber of the brain." He goes on to say that it is nothing but a lymph cavity, and in this he is unquestionably correct. Thus we see the anatomical research of the sixteenth and seventeenth centuries giving the *coup de grace* to the hypothetical psychology of the classical writers.

I must now pass on, but cannot leave Willis without drawing attention to the remarkable prescience and the logical thread of argument by which he comes to the most important conclusion, partly confirmed by modern research, that the office of the "cerebel"—*i.e.*, the small brain—is to be the source of involuntary actions, and, he adds, passions. Finally, he undoubtedly foresaw and clearly conceived the idea of what was regarded as the greatest discovery in neurology of the last hundred years—viz., the principle and theory of reflex action as established by Whytt in the eighteenth century. For he says, in speaking of the lower animals, which are destitute of developed brains: "So long, therefore, they being destitute of the internal principle of motion, move themselves all members only as they are excited from the impulse of the external object, and so sensation preceding motion is in some manner the cause of it." Nothing could express more clearly the whole position of what we mean by a simple reflex act, the principles of which underlie the function of the nervous system wherever such a system exists.

I take as my next landmark in the development of neurology the commencement of that feeling after the localisation of function, which is so well known

to you as the world-wide discovery of Sir Charles Bell.

Galen had already shown that there must be nerves of sensation and nerves of movement, but beyond Willis making it sure that the nerves did convey sensation and "instincts to movements," no further determination as to the particular part of the nervous system which might be occupied in providing for such transmission of sensations and movement was made until 1811, when Sir Charles Bell by his numerous investigations was led to believe that separate parts of the brain and spinal cord subserved these two functions. To put this matter on an accurate footing, he says himself that nothing but experiment could decide the point. He further states that, in his opinion, at that time it was too difficult to try experiments on the brain. He therefore began by experimenting upon the spinal cord, and he satisfied himself that there was such a differentiation of function in the spinal cord. While he was performing these experiments, he remembered that the spinal nerves had, as he says, a double root. He therefore laid bare the roots of the spinal nerves and irritated them, discovering thereby that it was the anterior which gave rise to movements in the muscles, and not the posterior. He says: "I now saw the mean-

ing of the double connection of the nerves with the spinal marrow." And, in truth, he had discovered the first experimental fact which established irrefutably the immense principle of localisation of function. For having thus demonstrated by the only method of proof possible that the conducting channels in the nervous system possessed differences of function, it was relatively an easy step for subsequent investigators to show that the nerve centres, to which those channels led, were also similarly gifted with the differentiation of functional ability.

Many causes, however, tended to hinder progress in this direction, and it was actually not till 1870 that the next absolute proof was obtained of the localisation of function, so far as the highest centres of the nervous system were concerned. In that year Fritsch and Hitzig discovered that electrical excitation, with minimal stimuli, of various points of the cortex, caused those storehouses, of which Willis spoke, to discharge, and to reveal their function by the precise limitation of the groups of muscles which they were able to throw into action. These researches were abundantly confirmed and greatly extended in this country by Professor Ferrier, and thus has been constructed in the history of this subject the most recent great platform or stage of permanent advance.

The details of this advance I shall give in the second course of these lectures, but it is impossible for us to follow them with any profit unless we have clearly established in our minds the basis of all nerve function—viz., reflex action; and to the consideration of that basis, with its beautiful development in the spinal cord, will be devoted the lectures of the present year.

LECTURE II.

We have seen how the earliest authors gradually determined that there were two great principles underlying the function of the central nervous system. The first of these was what we now call reflex action; the second, the limitation of the localisation of definite functions to special parts of the structure or system. Speaking popularly, by the term "reflex action" is to be understood simply the fact that the nervous system provides the necessary apparatus for enabling an animal to make a response in the shape of movement when it receives a sensory impression. I may remind you in passing, that an ejaculation, cry, or even connected phrases when made by the higher animals by way of such responses, are of course only movements, highly specialised no doubt in the last case I have imagined, but still only movements. To impress this still more upon you, I may remind you that what we call directing the attention is in its essential particulars a combination

of movements. As to the expression "localisation of function" it needs no further enlargement; the term sufficiently explains itself. These two great principles being clearly before us, we are enabled to proceed at once to the study of the nervous system as we see it in the lowest animals. For just as it was necessary for us to review the work of previous investigators, so it is now necessary for us to examine the function of the nervous system as it is exemplified in its simplest forms. Before, however, I actually enter upon the subject in detail, I must say a few words by way of prefatory caution. This caution refers to the hesitation which we ought to feel in regarding the objective phenomena presented by the lower animals, as resembling in their causation the similar objective phenomena which are evolved by our complex nerve systems, which we are able at the same time to analyse by means of subjective introspection. To make my meaning clearer, let me refer to a very popular illustration of this difficulty. The poet has spoken of the pang which a beetle endures, when suddenly exterminated, and has compared it with that suffered by a giant. Such a thought as this means that the phenomena of the nervous system of the lower animals only differ from those of the higher in quantity rather than quality, and is

an instance of the want of appreciation of the difference between the complexity which precedes the evolution of even elementary movement in the higher animal, and the simplicity, on the other hand, which underlies very similar movements when performed by a lower organisation. This want of appreciation has led to the employment of the term psychic or psychical activity in speaking of the deeds (*i.e.*, movements) of some of these latter. Thus the writer whom I have quoted obviously meant that, in his opinion, the causes of the objective phenomena observed were so similar in the two cases that we were to regard them both as identical. The logical fallacy, however, in such a view is obvious when we extend the point in the manner I have just indicated. But it is moreover, physiologically speaking, incorrect, because it implies that whatever difference there may be in the structure, the function remains the same, a conclusion which only has to be stated for its absurdity to be at once appreciated. When we therefore approach the study of the nervous system in the lower creatures, and note, while we observe what they do, that their acts, even the simplest, are very like what we see performed by the higher animal, we must never allow our judgment to carry us away, but we must always say at once to ourselves : What

are the events which have preceded the performance of that act?

This preliminary consideration will, I believe, enable us to avoid the danger of flying to the treacherous expedient of what is called a simple explanation, when we are still in ignorance as to some of the most important factors of the actions under consideration. To pursue this subject yet a moment more, I must bring to your notice the confusion of thought which has led to the employment of such terms as consciousness, volition, and purposive action, when speaking of the movements of even the simplest organisms. A vast array of writers have discussed the question as to whether we are to regard the lower animals as possessing, as they say, consciousness, and from this have even proceeded to formulate ideas as to whether they have a soul; while, owing to the remarkable discoveries of the physiologists, about forty years ago, as to the functional activity exhibited by the spinal cord of the frog when separated entirely from the brain, an animated debate was actually excited as to whether the spinal cord possessed the attributes of the mind. Speculations of this kind, however, are only rendered possible by the unjustifiable application of a metaphysical terminology, which was originally devised for the analysis of the

mental aspect of the most highly complex structure—viz., the brain of man, to the consideration of the simplest reactions of protozoa, small masses of protoplasm, and I do not propose therefore to waste time upon them at present, although at the close of this Session I shall briefly revert to this subject, having only touched upon it at some length now, because this first division of my lectures treats of the spinal cord and ganglia, round which the controversies I have described have so long raged. I would therefore ask you at once to dismiss from your thoughts any preconceived ideas on the point, and to come to the study of the facts that I am now about to describe without any reference to, or recollections of, those which are exhibited by ourselves or our mammalian congeners.

I shall begin by discussing the phenomena which are presented by the lowest masses of protoplasm that zoologists consider to be entitled to rank as animals—viz., the protozoa. These protozoa present sufficiently constant appearances to enable us to recognise them wherever met with, and they consequently are very properly divided into species; but when we come to look at them from the point of view of their possibly exhibiting nerve phenomena, they are so obviously elementary that we are not justified

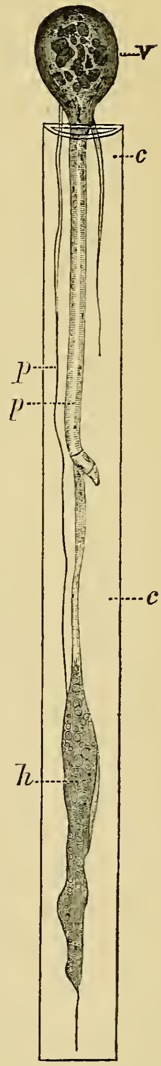
in considering their behaviour until we have devoted at least some little time to seeing what simple protoplasmic structures, which are not in the least suspected of having anything in the shape of a nervous system, will do under similar circumstances. The mere contraction of protoplasm in response to an external stimulus, whether that be mechanical, electrical, thermal, or optical, is exhibited by the protoplasm of botanical as well as animal structures. Thus, in the sensitive plant an external impression, such as a touch, is sufficient to produce movement of a most strikingly responsive kind. And if we examine the blood of the higher animals we find that some of the small corpuscles of that fluid are nothing but little masses of protoplasm closely resembling the lowest protozoa, and we further find that these little white corpuscles, or leucocytes as they are called, exhibit movements which in ordinary speech would be said to be purposive ; an expression, however, which would to my mind be very improperly applied. I have just given you an example of what plant protoplasm will do by way of response to an external stimulus, but the little leucocytes or white corpuscles of the blood apparently behave in a far more remarkable manner, an explanation of which, nevertheless, seems to be perfectly possible from purely physical considerations. Accepting the view

that all protoplasm is irritable—*i.e.*, capable of altering its form in movement, when any kind of physical or chemical change is wrought in it, the facts which are now so well established—viz., that if some injury or other sort of irritation be applied to the tissues, the leucocytes, instead of circulating freely within the blood-vessels, proceed to get out of them and to form, by their aggregation and subsequent liquefaction of the tissues, what we call matter or pus—become explicable by ordinary physical means. It has further been shown quite recently that if micro-organisms, which are themselves the sources of disease to the animal they invade, enter the system, the leucocytes go towards the micro-organism and apparently seek to destroy it. This has been fancifully regarded as a distinctly benevolent effort on the part of the leucocytes, but a more scientific investigation has shown, more especially by Dr. Massart, that the movements—*i.e.*, wanderings—of the leucocyte are determined by purely physical and chemical stimuli (chemotaxis), which I have not time to dwell upon now, and which have nothing in them of a purposive nature.

Turning now to the protozoa, we find that they consist, too, of masses of protoplasm, and that they are capable of pushing out long, limb-like protrusions of their body to gain food, &c. The movements of

these creatures for this purpose of feeding have often been compared to the purposive movements of the higher animals; thus, to give an example, Cienkowski has shown (see Fig. 4) that one species, *Vampyrella* (*v*), when wandering about algæ which are composed of tubes of cellulose (*c*) with a core of chlorophyll and other nutritious substances (*h*), if it comes opposite the open end of such a tube, down which its food may be lying at a considerable distance, it will nevertheless send down the tube a filament (*p*), having a length many times greater than the diameter of its own body, to reach the object of its search. This reaching out on the part of the animal to obtain that which it cannot come in contact with is looked upon by some as an evidence that the protoplasm is possessed of a sense perception, for the performance of which, however, no nervous system can be discovered in its tissues (Fig. 4). To take another illustration: Engelmann has shown that some of the

FIG. 4.



very lowest organisms, bacteria or microbes, are specially affected by certain rays of the spectrum; that one example, for instance, the *Bacillus photometricus*, when freely moving in a fluid through which the rays of the spectrum are sent, will collect itself only on the red side of the sodium line, and also in the ultra-red district. Finally, the plasmodium, or protozoon-like embryo of some fungi, will make advances clearly in the direction of nutritious substances, which are nevertheless at a considerable distance from it. All these phenomena, it will be at once seen, are instances of so-called selective action; but this is another example of an abuse of metaphysical terminology, because if we analyse them even to a slight degree, we are obliged to admit that they resolve themselves into those rather of adaptation and advantage—*i.e.*, efficiency of the life processes, chemical and physical, of the protoplasm itself, and that there is consequently no reason why they should not all receive interpretation in the direction of the at present ascertained laws of chemical affinity and physical influences, rather than by any more imaginative explanation.

So much for the example afforded by these animals of the first great function of the nervous system—viz., response to external stimulation; or, as it is

termed in the higher species reflex action. In character, the actions that we have just been considering, and which are evoked in response to obviously external influences, have a slow and a continuous development; but there is to be observed in the bodies of some protozoa a movement which is of a totally different kind, which is a distinct property of the protoplasm itself, and which, nevertheless, is regarded as being, in the higher animals, a clear evidence of the presence of a nervous system. In the substance of the protoplasm is to be seen a little space or vacuole. If, further, the animal be watched, it is seen that this little space quickly disappears, and then gradually develops again, to again disappear, and subsequently re-form. This alternation of appearing and disappearing is an example of rhythmical contraction of protoplasm. Such a rhythm must have a special causation, and according to most authorities it must have also a special apparatus for its fulfilment; and we shall discover directly, when we come to the higher classes of animals, that the ganglia are the instruments supposed to be specially arranged for this very purpose. In the body of a protozoon, however, no nervous system has ever yet been detected; but the fact that our present microscopes and means of research generally have not demonstrated its anato-

mical existence, is but negative evidence, and as such, most dangerous to be relied upon. As regards the causation of the phenomenon, it is true that in some instances foreign bodies have been seen in these contracting vacuoles, and noticed to have been expelled through a little orifice in the wall of the animal, as if the vacuole exercised a distinct function of getting rid of useless particles. If this be so, it is obvious that such particles might of themselves furnish the necessary irritation for the production of a contraction of the protoplasm, and hence that this would merely fall into line with ordinary response to external stimulation. But this explanation is obviously only applicable in a few instances. Summarising, therefore, the phenomena which are exhibited by these animals, and commonly regarded as significant of nerve action, we see that they are divisible under the two headings of—

1. Response to external stimulation.

2. The existence in the protoplasm of "spontaneous" rhythmical contractions.

We now pass to the cœlenterata, which are the next in order of evolution to the protozoa, in which we shall find that the two points we have just mentioned are not only much more highly marked, but that their existence is accompanied by the anatomical co-existence of a nervous

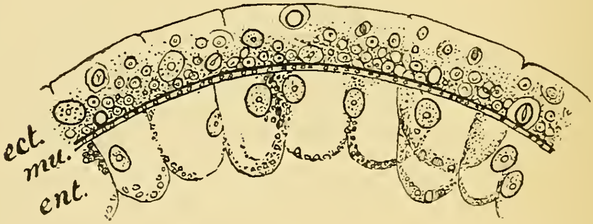
system. This last fact obtains double interest when we know that less than twenty years ago they were not supposed to possess one at all. This consideration, therefore, supported as it is by numerous other examples in the history of the progress of science, more than justifies the caution just expressed concerning the supposed non-existence of the nervous system in the protozoa.

We shall now spend some little time in the examination of what we may call the nervous phenomena exhibited by these cœlenterates or polyps, since we are fortunately in possession of a rich harvest of facts, obtained during the last fifteen years, most especially by the labours of my predecessor in this chair, namely, Mr. Romanes, as also by Professor Eimer, from the physiological standpoint, and by the brothers Hertwig and Professor Schäfer on the anatomical side. The cœlenterates are practically all tube- or bell-shaped animals, the cavity of the tube or bell serving impartially as a circulatory and digestive system. The tube forms are commonly spoken of as hydrozoa, and the bell-shaped forms as medusæ. Of the first sort the animal which has been most investigated is the hydra, which grows in our ponds and springs ; while of course the medusæ or jelly-fish are such common objects in the sea as to be familiar to all. These

two forms of polyps happen to illustrate two distinct aspects of an elementary nervous system so clearly, that I shall first speak of the hydra to emphasise my next point, and I shall then go on to describe the medusæ, their behaviour and their nervous systems.

The hydra simply consists of a tube, around the mouth of which are disposed numerous tentacles. When the body of the animal is suitably prepared

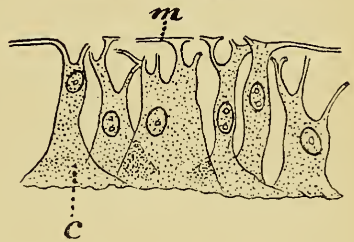
FIG. 5. (*Kleinenberg.*)



for the microscope, it is found to consist of three layers, all shown very beautifully in Fig. 5, which is a copy of Kleinenberg's plate illustrating his great work on the subject. The three layers, counting them from the exterior internally, are, first the ectoderm or outer layer (*ect*), which corresponds to our skin; next, the muscular layer (*mu*), which truly corresponds to our muscles; and, lastly, the entoderm (*ent*), which corresponds to our mucous membrane lining the alimentary canal. Now this animal, when the exterior of the body is touched,

reacts at once by moving. That is the first great principle that we have already seen illustrated in the protozoa. But Kleinenberg, by his anatomical investigations, found a most interesting arrangement of the simple cells (see Fig. 6) which build up the body of the animal, and which seem to provide us at once with the most diagrammatic substructure of the nervous system that could well be imagined; for he found, as is shown in the figure, that certain of the cells of the ectoderm (*c*) had processes (*m*) which ran into the muscular layer, while their outer portions—*i.e.*, those exposed on the surface—had distinctly a fibrillar appearance. He therefore spoke of these cells as neuro-muscular elements, and believed that here we had the same piece of protoplasm so modified that whilst its external part was calculated to receive and appreciate stimuli, these latter could pass down through its substance and gain the deeper processes, which upon the arrival of the stimuli would forthwith contract. So that, arguing by analogy from the anatomy and physiology of the higher animals, it was clear that, if this actually

FIG. 6. (*Kleinenberg.*)



was the function of these cells, we should have a truly fundamental representation of the nervous system for the provision of a muscular response to an external stimulus. Unfortunately, although this extremely simple view of Kleinenberg's* must be regarded as essentially correct in principle, as a matter of fact there is reason to believe that in the hydra there is not only distinct muscular tissue, but that there are also cells of the ectoderm which have more especially to do with the reception of impressions, and other cells which mechanically support the former.

In hydra, therefore, the matter is a little more complicated than was at first imagined, and we have special cells in the ectoderm which can be called nerve cells, and undoubtedly special cells in the muscular layer for the desired contraction of the body. In any case, however, as far as the physiological standpoint is concerned, we see here the beginning of a system which runs right up through the animal scale to man—viz., the provision of a sense organ, *i.e.*, nerve cell, in its elementary state in the periphery or external part of the body, which receives external impressions and communicates them

* Consult on this point Kleinenberg's paper, "Die Enstehung des Annelids, &c," in the Zeitschrift für Wissenschaftliche Zoologie, Band 44, 1886. Especially chap. v. p. 173.

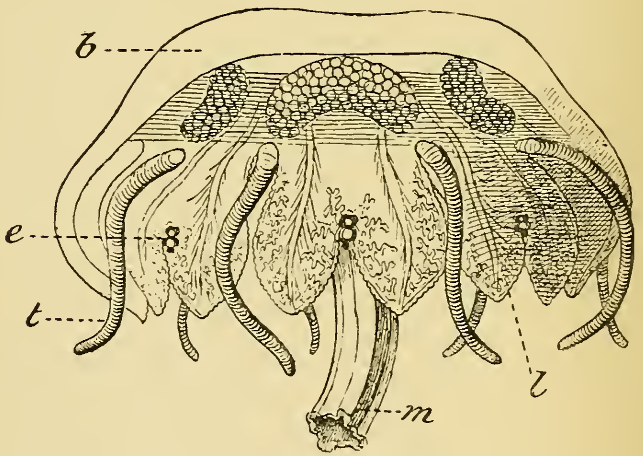
to the interior, with the result that a movement follows. We shall subsequently learn that in man the message is conveyed to the spinal cord, to the nerve cells there, from which it goes to the muscles. In hydra there is very little evidence that a nerve cell is centrally placed between the sensory cell in the skin and the muscle in the interior, though even in them this relation and interpolation of a cell is believed by some to exist.

We may now with advantage proceed to the medusæ, which must be regarded as higher in the scale than the hydra we have just been considering, and in which the interpolation of nerve cells indubitably occurs, thus introducing us for the first time to the structure and functions of ganglia.

A medusa consists of a bell of protoplasm (*b*, Fig. 7), which is beautifully shaped and divided into lobes (*l*), the margins of which form a continuous line round the lower border of the bell, and in the clefts between which are to be found certain little highly specialised portions of the ectoderm, which are undoubtedly sense organs (*e*). Between these, numerous tentacles (*t*) usually fringe the border, or there may be only a few, as we see in the following drawing taken from Haeckel's great work on these animals. Hanging from the centre of the concave or under side of the bell you see a tube-like process (*m*), which has

been variously termed the manubrium or polypite, and the interior of this terminates, below the summit of the bell, in a cavity from which canals radiate down the intervals between the lobes, and end at the margin of the bell in a circular canal which unites all the radiating branches together.

FIG. 7. (*Haeckel.*)



The tentacles and portions of the body generally are supplied with numerous little modifications of the ectoderm, which consist of sharp, long filaments, capable of being ejected from special little sacs, and used as weapons of offence and defence. It will be noticed that in this hasty sketch of the structure of a medusa we have for the first time had occasion to mention the existence of special sense organs. I

shall allude to the anatomy of these directly in further detail, when I come to point out the remarkable influence which they exert upon the nervous phenomena of these creatures. But I must also reserve that description until I give in detail the discovery of their nervous system as a whole. Meanwhile, I wish to lay before you, in exactly the same way as I have done with the protozoa, the physiological functions the medusæ possess, and we will later bring those facts into correlation with the structure that seems truly to be their source.

If a medusa is swimming freely in the sea, it is noticed that it moves along through the water by virtue of rhythmical contractions of its protoplasm—a property which we already observed to be present in the protozoa. By reason of the bell contracting and driving out the water contained in its interior the whole animal is impelled forwards, and the contraction being over, the bell intermittently expands again, water rushes in, and is again expelled. If the animal is irritated it discharges its little stinging filaments, the powers of which are of course familiar to every one who has provoked them. Looking at the animal therefore as a whole, it is evident that the predominant feature of the phenomena we have already considered is that of

rhythmical or intermittent movement. It also moves in response to an external stimulus, and this reaction and the discharge of its stinging threads are of exactly the same nature. But we must go further than this, because the distinctly radial arrangement of the animal, its division into lobes, &c., introduces us, as you may perhaps have already guessed, to the great principle of localisation of function. The simple proof of this is afforded by the following observation which Mr. Romanes, I believe, was the first to make—namely, that, if any given point of a medusa be touched, the lobes of the polypite which are nearest to the place irritated bend up towards it, and attempt to touch the selected spot. This experiment indicates that definite channels are arranged in the medusa for the conduction of impressions to and from certain points in its body, but this is of course nothing more nor less than the localisation of nerve function.

We will now examine the other predominant feature—viz., the Rhythm—because it was this striking phenomenon which led Mr. Romanes to the study of these interesting creatures, and enabled him to formulate several weighty conclusions on what are really the fundamental principles which underlie the action of all nerve systems. We

cannot therefore but profit very greatly by an attentive examination of his results, since if we thoroughly understand the *modus operandi* of the nervous system in the medusa, we shall only require a multiplication of similar units of knowledge to teach us the more complex details of rhythmical function in the higher animal. The rhythm of the contraction of the bell may be analysed, from several points of view, as follows:

1. Its source or initiation.
2. Its artificial production.
3. Its maintenance.

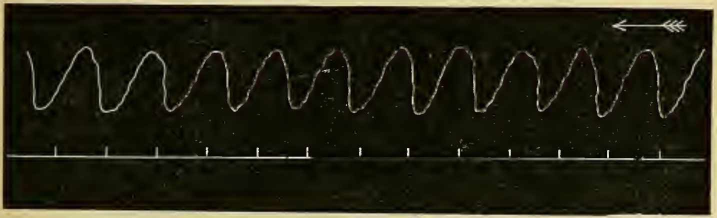
1. *Source or Initiation.*—The earliest experiments, both of Mr. Romanes and those made independently by Dr. Eimer, showed that the most excitable region of the bell was its margin, and that the natural wave of contraction appeared to pass up it from thence. But the actual proof of this region being the prime source of the rhythm was not forthcoming until the experiment of removing the margin was performed. This operation produces a cessation of the rhythm, and the motionless bell may be then said to be paralysed. The removal of the marginal bodies, customarily referred to as sense organs (see Fig. 8) produces a similar effect, and the inference that the region of these bodies is the important centre of origin of impulses, is

rendered still more obvious by the observation of Eimer, that if a marginal body and surrounding part of the umbrella or bell be excised and placed in suitable innocuous fluid, the part will rhythmically contract for ten days or more.

2. *Artificial Production.*—The further analysis of the rhythm was wanting, until Mr. Romanes proceeded to investigate the possibility of reproducing it in the paralysed bell of the medusa. This he found to be actually possible by exciting the motionless tissue with either a faradaic electric current or a chemical irritant like glycerine. The result was to evoke a remarkably regular rhythmical contraction and relaxation of the tissue. Such a re-awakening of the lost rhythm is a very remarkable fact, but its full discussion we must postpone for the moment. However, there is an all-important corollary to this experiment—namely, the question of fatigue. How far this element is present in relation to such a condition, and, if present, how far it goes to reveal the origin and nature of the (artificial) rhythm, must now be considered. Mr. Romanes found that if he caused the rhythmical movements to inscribe themselves by their raising a light lever which could write on a blackened moving surface, the result was a wavy line, as shown in Fig. 8; if then the piece of tissue were electrically excited for

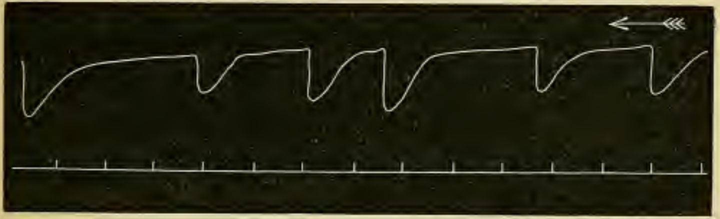
an hour, the trace became altered, and there ensued not only a change in the rhythm—*i.e.*, period of intermission—but also a change in the duration of each of the contractions (see Fig. 9). In five hours the tissue was quite exhausted.

FIG. 8. (*Romanes.*)



The lower line in this and the next figure indicates seconds of time.

FIG. 9.



This remarkable alteration of the normal movement is characteristic, we shall subsequently see, of the failure by fatigue of nerve centres, but we must not anticipate the general conclusions we are able to draw from these interesting results.

Mr. Romanes further found that warmth improved the rate at which the tissue reacted, but that heat

did not operate as a stimulus for origination of the rhythm.

This brings us now to the most important consideration as to how the rhythm is maintained, and whether that maintenance is co-indicated by any other phenomena.

LECTURE III.

It is impossible for us, with our present means of research, to determine exactly what maintains a rhythmical movement such as that exhibited by the medusæ, and we are consequently obliged to attempt the solution of the difficulty by indirect observation and reasoning. I have already mentioned one fact—namely, the influence of fatigue—and must now point out to you that contractile substance or muscle is far less easily exhausted than nerve centres. But we have a much more ready way of observing whether it is likely that the little marginal bodies which are undoubtedly the origin of the rhythm are also the source of its maintenance. This fresh method was also discovered by Mr. Romanes, and consists in an experiment of the following kind. The kind of medusa which is called *Sarsia* is a small bell from the centre of which normally hangs a short polypite. If now the marginal bodies and margin of the bell be

removed, it is then found that the polypite gradually relaxes and elongates itself to many times its previous extent. Using physiological language, the polypite was, before the operation, in the state called tonus—that is, moderate contraction, a character which it loses after the marginal bodies have been removed. The assumption is inevitable and correct that the marginal bodies are in the habit of maintaining this state of tonus. I think, therefore, we are perfectly justified in believing that they are similarly responsible for the maintenance of the rhythm. You will perhaps allow me to anticipate what follows in succeeding lectures by mentioning that the maintenance of this state of tonus in muscles is a characteristic property of the spinal cord nerve cells in the highest animals. To sum up, therefore, it is established that the duty of starting and maintaining the contractions of the bell in medusæ is relegated to the marginal bodies and tissue in their immediate neighbourhood.

The last property or function that I wish to refer to, or indeed which we know to exist in these animals, is that of localisation. They, as I have already stated, exhibit localisation of function in its simplest development. If a point on the bell be touched, the nearest lobes in the polypite bend up and fairly

accurately come into contact with the spot stimulated. This correct indication of the seat of irritation is of course a most fundamental factor in localisation.

To summarise, finally, the physiological properties of the medusæ which are referable to a nervous system, I would enumerate them as follows:

1. Response, by movement and discharge of stinging cells, to external stimulation.

2. Rhythmical movements of bell.

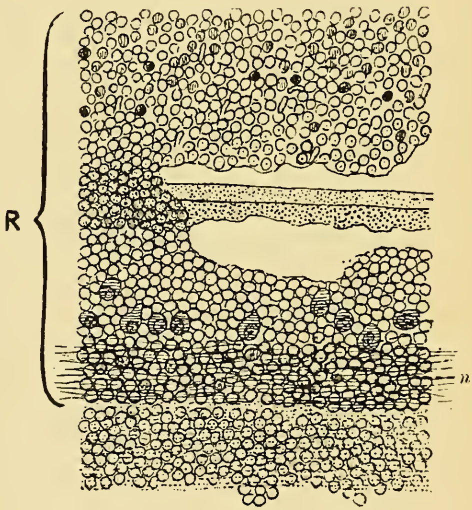
3. Maintenance of rhythm and of tonus.

4. Localisation of points stimulated, and coordinated movement adapted to the same.

Now having seen what these animals are capable of performing by way of (presumably) nerve function, let us proceed to examine the anatomical arrangement of their elementary nervous system. As an example I shall take an instance of one of the medusæ in which the small sensory marginal bodies are exposed, that is, not covered by the edge of the bell. In the first place, there is, running round the whole margin of the bell, a ring of nerve fibres mingled with cells. I have not yet described to you the structure of nerve fibres or of nerve cells, that I shall do directly; but you will understand that the fibres are exceedingly fine protoplasmic threads and the cells small nucleated protoplasmic masses. This is shown

in Fig. 10, representing part of the bell of a medusa flattened out, in which the general arrangement of this ring of fibres (n) and its relations are well marked (see also Fig. 11 *a*). In the first place, it

FIG. 10. (*Eimer.*)

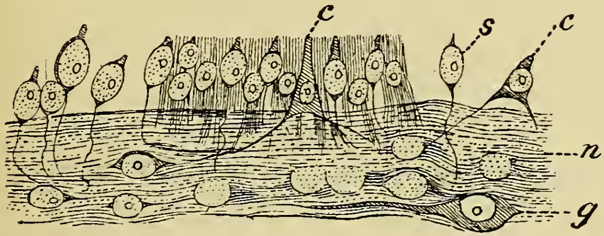


receives and gives fibres to each marginal body; furthermore, it gives also numerous branches which radiate upwards along the water canals that divide the animal into lobes. We will now turn to these structures more in detail. If we examine the fibres to begin with (see Fig. 10a, *f*), we see that

FIG. 10a. (*Eimer.*)

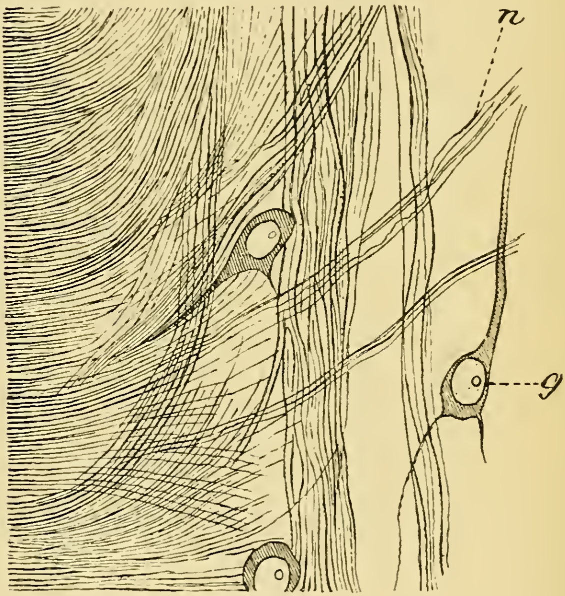
they are well-defined threads of protoplasm which present here and there little varicosities or swellings, and which nowhere possess any insulating covering of the kind such as one finds in the higher animals. They obviously start from and go towards the ganglion cells (*c* in Fig. 10a, *g* in Figs. 11 and 11a), and connect these latter with delicate cells in the ectoderm (*c* in Fig. 11), just in the same way as we have seen similar ectodermic cells of presumably nerve character to exist in the hydra. Now the ganglion cells, which are of the greatest interest because it is their function to store up and to give out nerve

FIG. 11. (*Eimer.*)



energy, are similarly rounded masses of protoplasm (see Figs. 10a and 11a), each with a large nucleus, and from their body run branches—usually two, rarely more—which continue into the surrounding

FIG. 11a. (*Eimer.*)

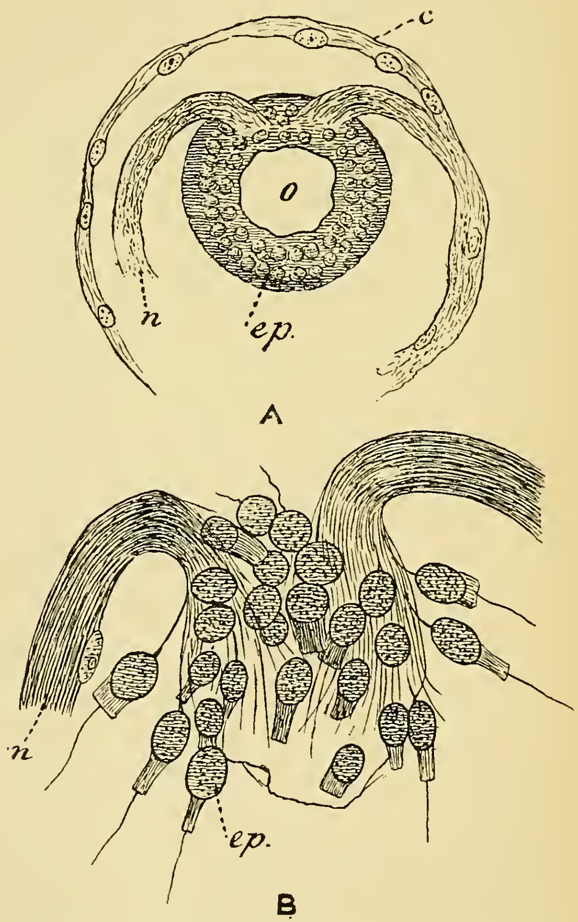


parts as nerve fibres.(*n*) These nerve fibres, that issue from the ganglion or nerve cells and pass to the muscle fibres, terminate in these latter in a peculiar manner, which we shall subsequently find to be repeated throughout the animal kingdom, and which simply consists in an enlargement of the protoplasmic thread into a little swelling, which may

also possess two or three small nuclei, and which is directly applied to the muscle fibre. I would ask your particular attention to this mode of nerve-ending of a fibre, inasmuch as it is believed by some to be just as capable of providing for rhythmical contraction in a muscle, as a ganglion or nerve cell, which is usually credited with that function. Now we come to the sense organs, which I have so often referred to as the marginal bodies (Fig. 7, *e*). These sense organs are remarkably simple in structure, and are adapted for the perception of *light*, of *touch*, and although we cannot in perfect truth add of *sound*, yet nevertheless they are capable of appreciating delicate vibrations. They consist of little finger-like processes of the umbrella tissue, into the centre of which is protruded a branch of the water canal or tube system. They are covered with ectodermic epithelium, which at the uppermost surface of the little protrusion is modified—*i.e.*, thickened and often pigmented. At the end of the organ the ectodermic cells are still more modified so as to form a little sac, as you see in this diagram (Fig. 12, A, *ep*), the cells of which are for the most part provided with cilia, and in the internal cavity of which are crystals (Fig. 12, A, *o*), which, by their movement against the delicate hair-like processes of the epithelial cells, evoke the perception of vibrations such

as the animal may experience when swimming in the water. The water-canal tube is of course lined

FIG. 12. (*Eimer.*)



by the entoderm, and between the entoderm and the ectoderm we have numerous nerve fibres (n) running

down from the nerve ring I have just spoken of above, to terminate in the ectodermic cells (*ep*). The rest of the general surface of the animal is sensitive to tactile impressions, and as the ectoderm contains numerous cells (see Fig. 11), from which fine processes can be traced into the nerve ring (*n*, Fig. 11) and plexuses (*vide infra*), these specialised ectodermic cells have been justly called nerve epithelium and regarded as sensory nerve-endings. Finally, the whole of the muscular tissue in the under part of the bell is overlaid by a very delicate and richly interlacing supply of nerve fibres, among which may be found also ganglion or nerve cells. Knowing now all these elements to exist, we may reasonably suppose that the schema of the nervous system in the medusæ is that of elements arranged in the following line:

Ectodermal sensory nerve cell.	Nerve Fibre.	Nerve ganglionic corpuscle.	Nerve Fibre.	Nerve-ending (motor).	Muscle Fibre.

All that remains now is to connect the facts, so far as we know them, of function with the observations we have just detailed of structure. That the medusa in the first place reacts to an external stimulus by movement, and that nerve excitation underlies that reaction is obvious enough, as follows. An excitatory state is induced in the

ectodermal or sensory nerve cell. That excitatory state is conveyed along a nerve fibre to a ganglion cell, the ganglion cell is similarly thrown into a state of excitation and communicates its condition, or, to use other language, discharges its energy down a nerve fibre to the nerve-ending of a fibre, and that nerve-ending causes the muscle fibre to contract. Thus far all is easy, but now we come to the question of rhythm—viz., the intermittent expansion and contraction of the bell. The question before us to decide is whether the ganglion cells perform the necessary alternate storing up and liberation of energy, or whether it is *not* the ganglion cell that does this, but possibly rather the nerve-ending, or even the muscular contractile tissue itself. A former lecturer at this institution, Sir James Paget, formulated forty-four years ago his belief that rhythmic motion is "an issue of rhythmic nutrition, that is to say, in which the acting parts are at certain periods raised with time-regulated progress to a state of instability of composition from which they then decline, and in their decline may change their shape—*i.e.*, move —or as nerve centres may discharge nerve force." There is no question but that this view is correct as far as the necessity of the state of nutrition of the apparatus alternating with the exercise of function goes, but there is great question as to which of the

elements it is in the whole apparatus that is the seat of this instability. This problem, as I said just now, has always excited the attention of physiologists, and numberless attempts have been made to arrive at a correct answer; but you will understand immediately how it is that I am unable to tell you what that answer should be, when you remember that science has not yet discovered any means whatever of measuring the amount of nerve force produced in a nerve fibre at any given time; we can measure its rate; of course we know, for example, that excitatory processes in nerves flash along them at about thirty-three metres a second; but we do not know at all how to reveal by physical methods the nerve discharge itself. Moreover, it is only within the last forty years that we have had any indication as to the frequency with which nerve impulses pass along nerve fibres—I mean by direct examination of those fibres themselves. It will be obvious to you that if what we want to know is how many times a ganglion cell of simple nerve centres, like those of the medusæ, discharges energy down nerve fibres to cause muscles to contract, it is no good our simply trusting, as has been done for many years, to watching and counting the duration and number of contractions or movements which a muscle makes, but we must rather find out some means of examining

the nerve fibre itself, as only in that way shall we discover whether the rhythmical contractions of the muscle are due to the ganglion cell or to the nerve-ending, or to the muscle fibre. Now the way in which the existence of the nerve impulse in a nerve fibre can be exhibited is that discovered by du Bois Reymond—namely, the detection of a change in the electrical state of the nerve fibre. This change always occurs when a nerve fibre is excited; if therefore we could get at the nerve fibres coming from the marginal bodies of the medusa, and if we could without error connect those fibres to a sensitive galvanometer capable of revealing such slight electrical changes as those mentioned, we should at least discover whether the marginal bodies gave out nerve discharges at regular intervals to cause the muscles to contract in the rhythmical manner already described. Unfortunately, at the present moment this cannot be done without considerable chance of error, but it is a subject well worthy of further investigation. In the absence of such direct evidence we must content ourselves with reviewing allied facts which can be obtained from the physiological researches which have been directed towards the elucidation of this question. I have already mentioned one most important circumstance—namely, that the artificial rhythm is soon exhausted, relatively

speaking, and will therefore only repeat that this points strongly to the assumption that the nerve cells, which are the more delicate and more easily tired elements of the apparatus under consideration, are the special instruments necessary for the production of a rhythm. But there are other facts to which I shall have occasion to refer in greater detail before the present series of lectures is terminated. I allude to the well-known observations of Stirling and others, which go to show that the nerve or ganglionic cells in the spinal cord of a frog (and the same may be added for mammals) are capable of storing up and accumulating excitatory changes which may not be enough to cause a discharge of the whole apparatus, but which nevertheless, by summing themselves up together in the nerve cell, ultimately get headway enough to lead the nerve centre to liberate its energy, and if (as was the case in Mr. Romanes' experiments) the stimuli employed are submaximal and constantly applied, it is clear that we may have been dealing with a provision of the same nature, and consequently have recorded a similar result.

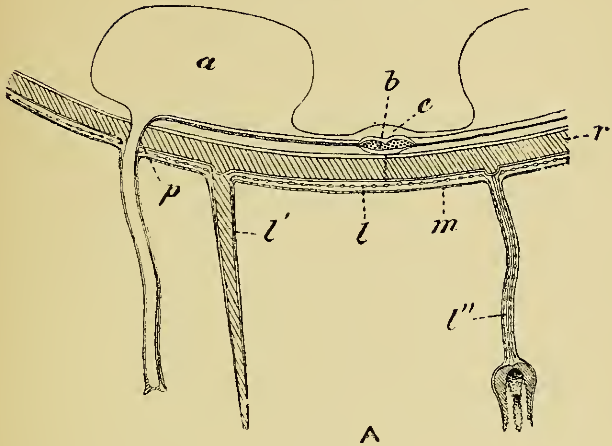
Quite recently, however, it has been suggested, on the strength of carefully performed experiments, that the rhythmical variations which can be detected in the contractions of the muscles in the higher animals, when thrown into action by their

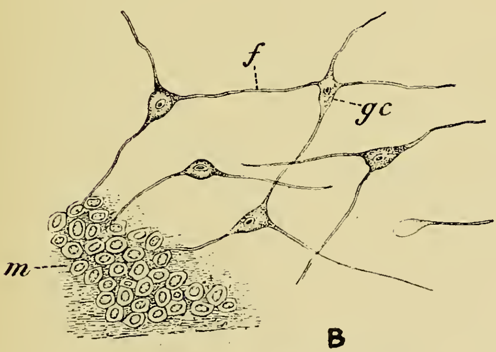
nerve centres, are due to a storing up by the nerve-ending. These experiments, which have been performed by Professor Wedenski, of St. Petersburg, need a most careful revision and repetition; but the fact of their having been made must cause us to hesitate in our interpretation of the phenomena seen in the medusa, especially since this animal possesses nerve fibres and endings just like the higher kinds. Numerous observations have been made on contractile tissues in parts of other animals, which are regarded as being without nerves; but all evidence of this kind rests on the fact that no nerves have as yet been discovered—in other words, negative evidence. I do not think, therefore, it is of any use to discuss them further in this relation. That nerve centres—*i.e.*, collections of nerve cells—do rhythmically discharge, has recently been proved by Professor Gotch and myself, by examining the condition of the spinal cord when the centres of the cortex of the brain were excited, and observing the electrical changes that occurred in the fibres leading from these centres. Lastly, the maintenance of tonus—*i.e.*, moderate continued contraction of the muscles to preserve the shape and proportions of a body—is known in the higher animals to be unquestionably due to the action of nerve cells in the spinal centres; for if in one of the

higher animals the nerve fibres, running from the centres in the spinal cord to the muscle, be divided, we find that the muscle, instead of presenting a firm contour due to moderate tonic contraction, is relaxed and soft in the paralytic state thus evoked. In conclusion, therefore, it seems to me that while for the present we must keep our minds open on this very interesting and important subject, the weight of evidence does seem to show that the rhythmical movements of these relatively lowly organised animals are due to their possessing a nervous system. I wish very much that it were in my power to have spoken more positively on this point, inasmuch as we are now, on the threshold of our subject, provided with simple and easily comprehended facts, and we might justly have hoped that science would have provided us with an easily mastered alphabet of nerve function. But such is not the case. We must therefore pass up in the scale to the next order of animals, which shall reveal to us some fresh factor of nerve function, and those which most conveniently follow the cœlenterates are the echino-dermata—that is to say, the star-fish and sea-urchins. Though not far removed from those beneath them, these animals nevertheless are higher, and, what is much more important to us, they have also been physiologically

investigated by Professors Romanes and Ewart. As just suggested, they indicate to us, for the first time distinctly, what we commonly call co-ordination, when speaking of the action of nerve centres in the higher animals. This expression, co-ordination, is frequently improperly employed; but it is a very useful one, if its meaning be carefully limited to express the successful co-operation of nerve centres when simultaneously excited in greater or less degree. Now of course this phenomenon is undeniably present in the medusæ, since without it the localisation of function which they reveal would be practically impossible, and it is presumably provided for by the ring of nerve fibres which connect the marginal bodies one with another. But, in the medusæ, the intimate relations of different parts of a body are so developed, that division of these ring-shaped connections does not obviously disturb the general functions. It is, however, otherwise with the echinodermata. In a medusa the bell, although divided into lobes, habitually moves *en bloc*, and consequently we do not have that differentiation of nerve function which demands differentiation of structure. But in the case of the echino-dermata, we have as a rule to deal with animals built on a radial plan in more or less rigid shells (Fig. 13, A, *r*), but whose whole body and radial structure, may in special cases be so

FIG. 13. (*Romanes and Ewart.*)





A. Vertical section of wall of an echinus.

a = Water canal.

l, *l'*, *l''* = Point to the nerve plexus on the outer surface of the shell, on a spine, and on a pedicillaria, respectively.

B.

gc = Nerve corpuscle.

f = Nerve fibre.

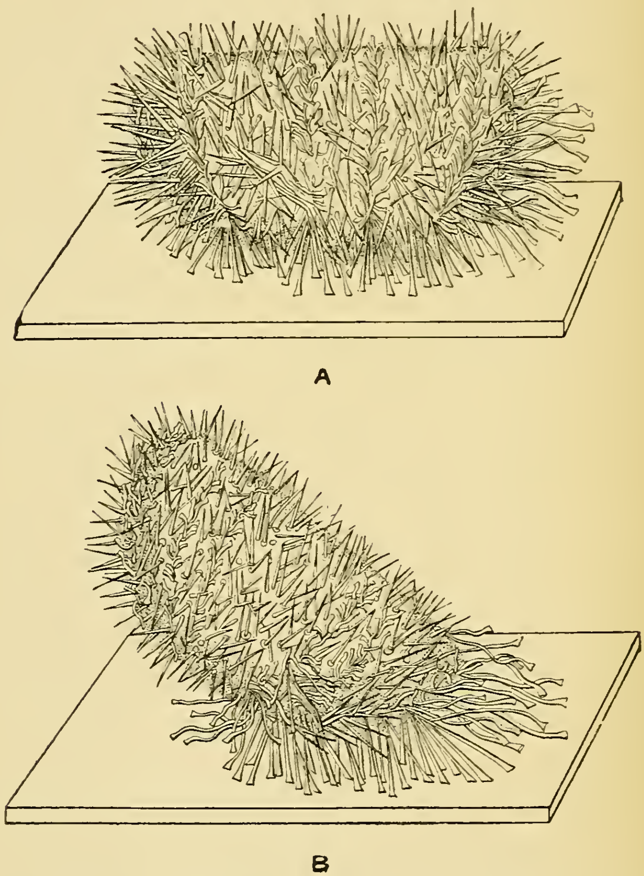
B is much more highly magnified than A.

divided and the shell flexible, as to give their individual parts a special independence, in addition to the capability of harmonious co-operation for the good of the organism as a whole. Briefly outlined, therefore, these animals may be described as possessing a radial structure, for the most part strengthened by a shell covering, in the radii of which are developed nerve channels and water vascular channels, these latter terminating in numerous distensible and protrusible feet and sucker-like branches (Fig. 13, A, *p*, *l'*, *l''*). In the centre of the body and on its surface occurs the elementary nervous system, which is more developed than in any animal we have yet studied in the present course. As you see in Fig. 13, the nervous system in its essential details, is arranged, like that of a medusa, into a system of plexuses and cells (see Fig. 13, B, *gc*), aggregated under the ectodermal epithelium, and also joined by branches to a nerve ring (Fig. 13, A, *b*) which runs round the central axis of the body. Considering that this ring is connected with branches coming from all parts of the body, considering also that it is united to a system of plexuses on the inside of the animal and on the outer side (*l*), it clearly takes the place of an apparatus for the complete co-ordination of the various nervous phenomena exhibited by it. These

nervous phenomena we must now for a moment discuss, remembering that the echino-dermata, like the medusæ, possess perceptive organs and ectodermal epithelium cells, which are capable of receiving impressions, and also of appreciating sensations of tension, strain, &c. Owing to the physical necessities or arrangement of the parts of the body, the objective phenomenon of movement in these creatures is of a very specially slow, deliberate, weak, and imperfect execution; but, such as it is, it is quite marked, and enables us to appreciate the difference between this kind of animal and one like a medusa. The accompanying photographs (Figs. 14 and 15), from Messrs. Romanes and Ewart's paper, exhibit the actions of a sea-urchin in the normal state, trying to right itself when it has been laid on its back. You observe that it puts forth its sucker-like feet at one end, laboriously tilts up its shell until this latter rests imperfectly on its edge (Fig. 15, A), and then proceeds by the same means to lower itself down again (Fig. 15, B). Now this apparently simple action, we shall see, is lost when the factor of co-ordination is destroyed. But let me first say that Messrs. Romanes and Ewart found that the echino-dermata exhibit naturally, as you would expect, a simple response by way of movement in answer to an external stimulus.

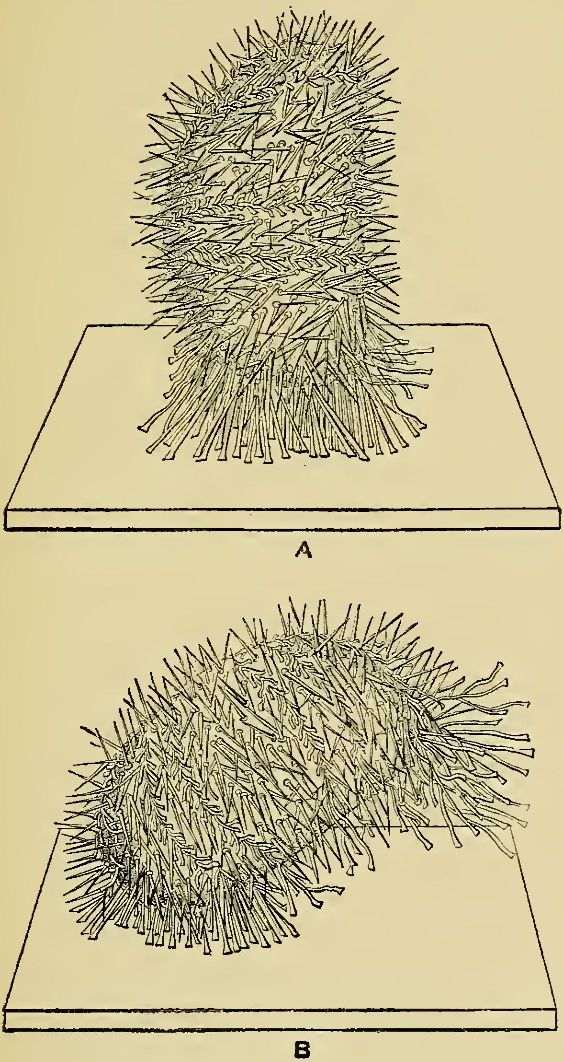
They noted, in passing, that the animal always moved in a line directly away from the source

FIG. 14. (*Romanes and Ewart.*)



of excitation. Further, that a touch on the surface of the body was correctly localised. To turn now to the actual experiments. The above-

FIG. 15. (*Romanes and Ewart.*)



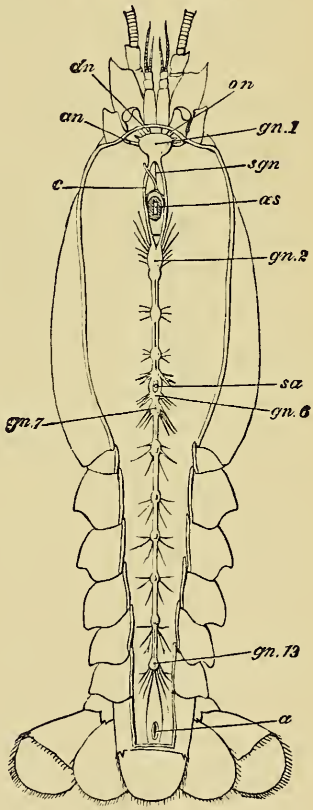
mentioned authors found that if the ring which unites the various divisions and branches of the nervous system were divided, thenceforth the animal had no power to right itself, or only a very incomplete power to do so, the fact being that the plexus of nerve fibres on the outer surface of the body was sometimes capable of subserving the duties of co-ordination. That is to say, the movements of the feet, and the movements of the spines, which are a kind of helpers or crutches to the feet, are to some extent co-ordinated by the plexus of the inner surface of the shell. This inner plexus again is to a great extent dependent for its efficiency on the activity of the central ring, though it is also capable of considerable power of co-ordination. We have therefore in the ring of nerve fibres the first construction of a centre for co-ordinating nerve impulses and producing co-operation. In animals a little higher in the scale, indeed those which we are about to study next, this factor of nerve function—namely, co-operation—is not only the most interesting, but is also very highly developed, and we shall find that it is in them, not, as in the echino-dermata, a simple matter of a ring which connects together, somewhat vaguely perhaps, radiating trunks of nerve fibres, but that it consists in the development of what are called commissures—that is to say, direct channels

uniting two nerve centres in one direction for example, and then others for connecting them with neighbouring nerve centres on either side. When we examine the whole mechanism in the echino-dermata anatomically, we find that on magnifying the tissues highly, the nervous system, as in the medusæ, is made up of sensory cells and organs, fibres, ganglion cells, &c., and this nervous ring, which is so important to this animal, and is chiefly composed of ganglion cells and fibres, just like the nerve ring running round the margin of a bell in the medusæ. To study now this new accession to our knowledge of nerve function—namely, the co-ordinative action of the nerve centres one with another—we must leave the echino-dermata and proceed to the consideration of the arthropoda, which include, of course, the jointed animals such as the lobsters, and their congeners, the innumerable insect forms. These animals, by virtue no doubt of an improvement in the organisation of their nervous systems, as well as the more practical development of their motile parts, exhibit, as representative of the objective phenomenon of movement, characteristics far different from those we have so far been studying. This specimen, for example, of daphnia that you see darting hither and thither in the water, illustrates very markedly this striking difference.

You will notice that this transparent little creature reveals the general structure of this class. You see that the body is surrounded by a hard shell, that there are well-developed sense organs, those for touch forming beautiful antennæ, while sight is provided for by a compound eye, the visual impressions being transmitted to a nerve centre which is situated just above the throat. Now let me say at once that from henceforth we shall speak of nerve centres in these animals as ganglia. We were not able to do so while speaking of the nerve cells which are distributed so freely and generally along the nerve rings in the medusæ and the echino-dermata. But in the arthropoda the nerve cells are not scattered in a haphazard way, but are collected together in different masses, wrapped up and bound together by connective tissue, while the nerve fibres which enter and leave them are gathered into very distinct cords or bundles, as you will see directly. Consequently it is convenient to have some generic term to express these collections of nerve cells. They are therefore spoken of as ganglia. Further notice that in this daphnia we have, for the first time, a blood circulation to nourish all the complex parts of the body. You see pulsating behind this tube, which is the digestive canal, a very definite heart. The other ganglia and nerve fibres which are in connection

with the ganglion in the head are not so readily visible. This last point, however, is more easily demonstrated in the larvæ of some of the higher forms of arthropods. In, for example, the animal *Corethra plumicornis*, we have a segmented shell, the head, which has eyes, is furnished with filamentous appendages, and, further, the throat and the rest of the digestive canal are very well marked, so that we can see above the former of these a large ganglion, and then, running down the underside of the body, a chain of ganglia, and a commissural chain (*c*) of fibres connecting them. From the study of these little animals we are able

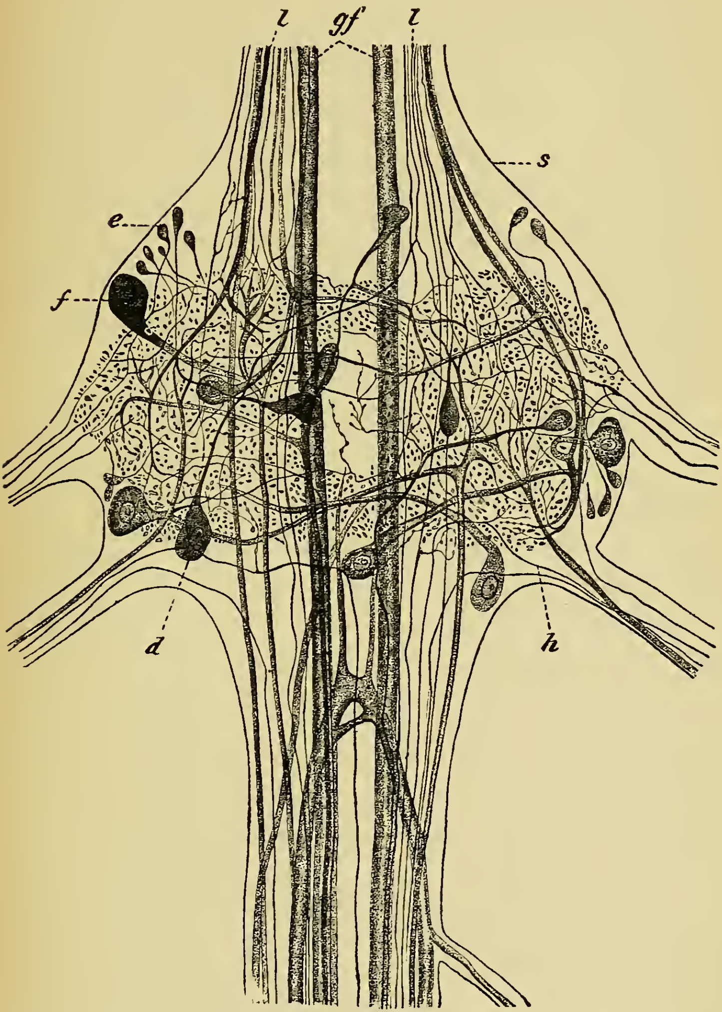
FIG. 16. (*Huxley.*)



to proceed with advantage to investigate larger specimens, of which the simplest is the crayfish. Fortunately, too, Professor Huxley has made it the subject of one of his lucid and most plea-

santly instructive zoological monographs, suited for all readers, so that those who wish to pursue the subject further can do so with the utmost readiness. In Fig. 16 is given diagrammatically a dissection of a crayfish, showing the nervous system and its relation to surrounding parts. You will notice that in the forepart of the head is situated a large ganglion (*gn. 1*). This ganglion receives nerves coming from the eyes and the antennæ, and gives nerves to the foremost of the head appendages. Running backwards from it are two bundles of nerve fibres, or commissures (*c*), which, passing on each side of the mouth, connect the large head ganglion with the first (*gn. 2*) of a series of ganglia which are arranged all down the front of the body just inside the shell, and which correspond one to each segment. The whole of the nervous system in this animal, it must be distinctly understood, is paired—that is to say, each ganglion, as I have just described it, really consists of two ganglia connected by a little short commissure, or bundle of fibres; consequently the commissures which connect the one paired ganglion of one segment, with the next paired ganglion of the segment below. are double, simply because of two sets or collections of nerve cells, one for each of the two halves of the body (Fig. 17, *l*, *l*). There is nothing for us specially to note in the structure of the nerve fibres or of the nerve cells

FIG. 17. (*Retzius.*)

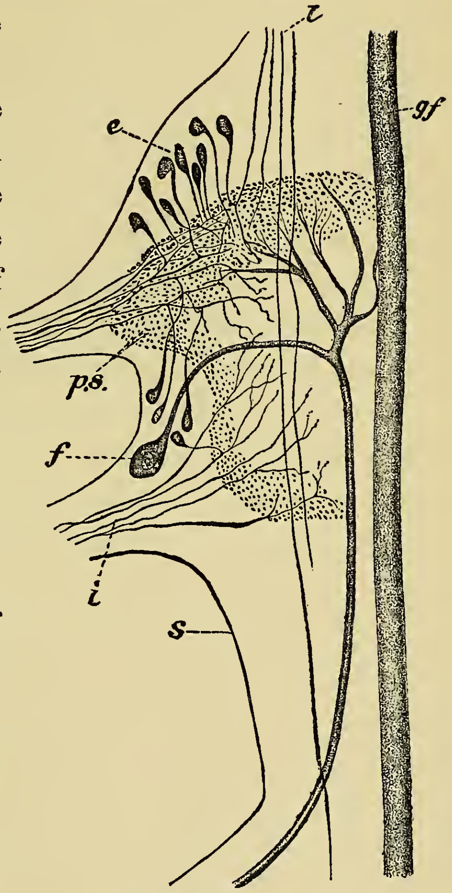


in the arthropoda, but each of these elements are better developed and more differentiated, perhaps,

than those seen in the lower orders. The minute structure of these ganglia has been made an elaborate study by Professors Retzius, Biedermann, and others. From the splendid work of Professor Retzius is taken Fig. 17, representing the appearance of the first abdominal ganglion in its sheath (*s*) when stained with an aniline dye, which is practically taken up by the nerve tissues only. The longitudinally directed fibres (*l*, *l*, *gf*), which form the commissures just spoken of, are seen to be largely developed, but the point of greatest interest and importance is the fact (shown also in Fig. 18) that the nerve fibres (*i*), entering the ganglion, terminate or arise from numerous side branches, which are lost in the granular (punctate substance) (*p*, *s*) material, which forms the groundwork of the ganglion, and that their connection with nerve corpuscles is, as especially shown in Fig 18, of a lateral or T-shaped character. Thus there is no evidence here of direct connection between the nerve fibres or processes of one nerve cell with those of another. Fortunately we have definite observations made on these simple ganglia by the experimental research of physiologists, and principally by the investigations of Mr. Ward. This author first devoted himself to finding out whether the function of co-ordination was disturbed when the commissures uniting the ganglia were interrupted, and he

found that it was so. That if the fibres, for example, connecting the large ganglion with the second were divided on the one side, initiation of movements of limbs of that side was lost; but of course if any of the limbs were touched, there was a simple response in the shape of movement. If both the commissures are divided, there is complete loss of initiation. Under these circumstances, the legs when irritated move, or the chelæ, if touched with objects, react at once by grasping them

FIG. 18. (*Retzius.*)



e = Peripheral small ganglion nerve corpuscles; note their T-shaped junctions with nerve fibres.
ps = The punctate or ground substance.
f = Large nerve corpuscle, also joined at right angles to a large fibre.
gf = Longitudinal commissural giant fibre.
l = Fibres of longitudinal commissure.
i = Ingoing nerve fibres.
s = Sheath of ganglion.

and conveying them to the maxillipedes, which hand them into the mouth; but the animal exhibits no regard to the nature of the food, and similarly shows no regard to its position, provided the water in which it is placed is motionless, further, if reversed, it is impossible for it to replace itself, as, in its normal condition, it usually does immediately. It is interesting to note that the lower ganglia, after the influence of the highest is thus cut off, when moderately irritated caused rhythmical movements of the posterior or ambulatory legs. We thus see that the highest ganglion is the most important, and corresponds somewhat to the brain of higher animals. It nevertheless is not entirely so, for, as just described, some co-ordinated movements of the legs and of the jaws in feeding can be performed, even if the uppermost ganglion have disappeared. If now, however, the second ganglion's influence is removed by dividing the commissures connecting it with the third ganglion, the power of moving the jaws in feeding disappears so far as it is co-ordinated with movements of the limbs, and it is clear therefore that these two first ganglia exhibit in a remarkable way that great principle of nerve functions of which we have as yet seen but little—namely, the precise localisation of action in definite parts of the nervous system, or, as one

naturally prefers to say, in special nerve centres. We are also justified from these experiments in concluding that, in these animals, the nervous system in each of its conjoint halves subserves practically the functions of only that side of the body in which it happens to lie. We have therefore not only localisation of function, but also proof that, in the systems in which that is first well marked, there is concurrently exhibited a unilateral character of the representation of movement in the nerve cells.

LECTURE IV.

After the review that we have just made of the nervous system and its functions in the invertebrata, we are now justified in passing at once to the vertebrata. In order to utilise most profitably the time at our disposal, I shall proceed to describe to you the anatomy of the spinal cord and the ganglionic arrangements of three classes of vertebrated animals, and I shall point out to you the relations which those structures bear to the peripheral nerves of the body, before proceeding to explain to you their function. This course is not only natural but inevitable, because while we have a large amount of experimental research bearing upon the function of the spinal cord, it has been derived from observations upon different classes of animals; and this, according to the principles which we have already had occasion to find true, means sufficient difference in function to necessitate caution in the interpretation of facts. As specimens of vertebrated animals, besides man and apes, to which I shall make

reference, I shall employ only three, as I have just stated—viz., the amphibia, birds, and carnivora. The anatomical structure in the last order is so very near that of the higher animals, including man, that very reasonable and accurate inferences have been successfully drawn from their examination in making comparison with the higher orders. In all cases, where we are dealing with the function of similar organs in different orders of animals, we can avoid error if we classify the points to be elucidated into a first division of general principles, and follow that by succeeding divisions, gradually introducing more and more details. What is true of one order as regards the first of such divisions, is undoubtedly true of another; but where mistakes have been made they have followed the indiscriminate application of facts from one animal to explain events occurring in another, without reference to the division of principles such as that I have indicated. With this prefatory caution we can very well proceed to our task, without fear of confusing incompatible facts.

It will first be necessary for us to consider what we have rather left out so far—viz., the structure of nerve fibres, which we now know to be particularly important, because of late years, chiefly through the researches of Gaskell, the mere differences in

size of fibres in the mammalia have been shown to be determined in part by differences in function. Of course in the amphibia it is especially easy to study these structures, both in their anatomical and physiological relations, since they preserve their characters unaltered for some time after general death. I shall therefore show you some specimens of nerve cells and nerve fibres taken from the frog.

Nerve fibres are divided into two classes, which are termed respectively medullated (Fig. 20) and non-medullated (Fig. 19). This distinction is drawn because in the first class the fibre itself—that is, the nervous cord—is, just as in the second class, merely a fine thread of protoplasm, but happens to be also surrounded by a sheath of insulating material. You see these fibres here in the living state unaltered, but it is easier to demonstrate this sheath when the fibres have been stained, as in the present instance (Fig. 20), with osmic acid, which colours the insulating sheath black, owing to the fact that this latter is of a fatty nature. The other class of the non-medullated nerves, when thus treated with osmic acid, simply stain of a light brown colour, as they do not possess this insulating sheath. Now, Gaskell has shown that those fibres which have no sheath have always come into con-

nection with ganglia after they have left the central nervous system, and before, of course, they reach

FIG. 19.

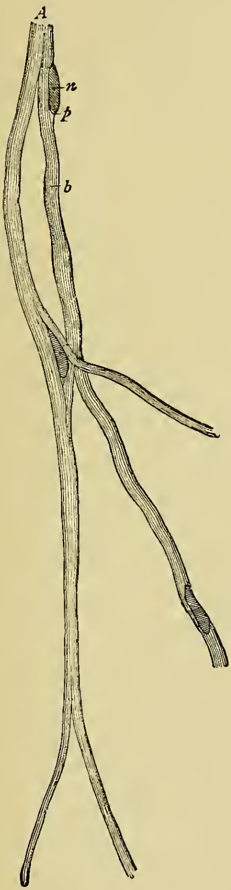
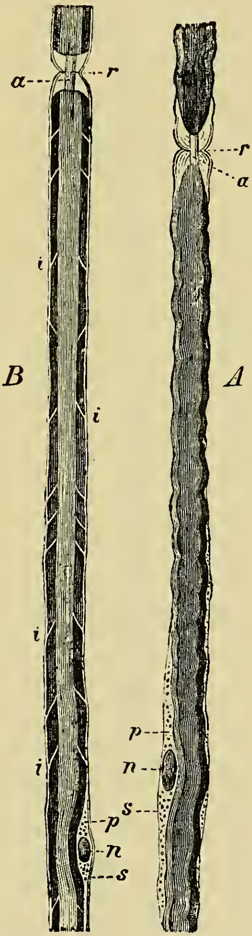


FIG. 20.



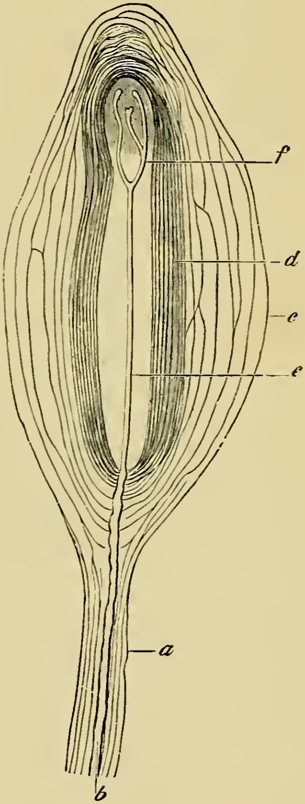
their destination, and, consequently, that the loss of the sheath is an evidence of this junction. Of

the meaning of the sheath or its utility we know nothing, but it is supposed to act as an insulator. I shall now speak of the destination of nerve fibres. You have seen sufficient to know that, whatever be the structure of the nerve fibre, it either conveys an impression to the central nervous apparatus or away from it; in other words, it is, as in the first case, a sensory fibre, or, as we ought more correctly to call it, an *afferent* channel, whereas in the second case it is a motor fibre, or an *efferent* channel. Taking the first set of fibres, the afferent channels, we find, of course, that we thereby include all the nerves which convey special sensations—the optic nerve or the nerve of sight, the auditory nerve, and so on—not to mention the innumerable ones which run from the vast multitude of tactile sense organs that are scattered over the skin. I cannot detail to you the structure of all these, nor is it necessary, since they are to be found described at length in every text-book of anatomy;* but it is incumbent on me to give you an idea of sensory nerve-endings and the general principle on which they are all constructed in vertebrate animals. Viewed in its simplest condition, a nerve fibre which is capable of receiving a sensory impression terminates in a little bulbous expansion (Fig. 21, *f*), and this bulbous

* Consult especially Quain's "Anatomy."

expansion is very frequently ensheathed in various ways for a purpose which is not fully understood, but which seems to have something to do with excitation of the nerve fibre. I here show to you, as an example of a sensory nerve-ending, one of the beautiful little bodies which are to be found in the substance of our fingers, and are distributed throughout the vertebrate animals, and which unquestionably are organs for the reception of touch, as also, possibly, for temperature sensations (Fig. 21).

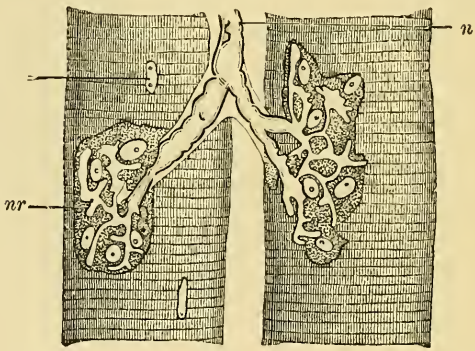
FIG. 21.



You will observe that we have, entering the lower part of this oval body, the nerve fibre (*b*); it passes up through the middle of the body, which, as may now be mentioned, derives its name, Pacinian corpuscle from Pacini, the Italian anatomist, who, simultaneously with the late Mr. Marshall, discovered it. Ensheathing the nerve fibre are concentric

layers of altered protoplasm (*c*, *d*) which, while protecting its delicate bulbous end are not known to exert, as just stated, any very definite influence upon it. A sensory nerve-ending therefore, briefly summed up, consists of a bulbous end to the nerve fibre, more or less concentrically ensheathed.

FIG. 22.



We now turn to the other side of the system, to see how a nerve fibre terminates when its destination is muscle or contractile tissue (see Fig. 22). I have shown you how that, in the medusæ, the nerve fibres that are distributed to the muscular tissue of the bell terminated in little nucleated swellings. We now find that exactly the same conditions, in varying degrees of complexity, prevail throughout the animal kingdom up to and including

man, the nerve fibre (n) which arrives at a muscle fibre swelling out into a little protoplasmic cushion (nr), which is attached to the side of the muscle fibre in intimate contact with it (Fig. 22). That the nerve fibre and its ending have rather different properties is known to us by the action of certain drugs which have been found to paralyse the action of the latter, but not the nerve fibre itself. It is clear, therefore, that these nerve-endings do possess a kind of physiological individuality, a matter to which you will remember I was obliged to direct your attention in speaking of the source of the rhythm in the bell of the medusa.

I shall, however, leave the particular points which will interest us in the function of nerve fibres, until after we have further considered the anatomy of the nerve centres, so far as it involves the spinal cord and so-called sympathetic system.

To this subject we will now turn, and, taking the frog as the most convenient example and as the animal about which we know most, we find when we come to investigate its nervous system, and to compare it with the lower orders we have already considered, that it is not possible for us to draw any but very general conclusions, respecting the comparisons which we strive to make between the complex system which is now introduced to our

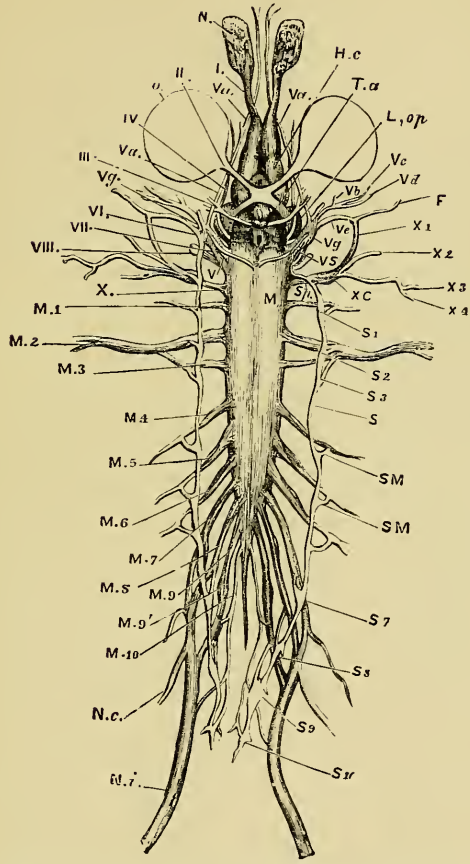
notice and the simpler apparatus which I have been describing. At this moment this question is being very hotly debated, chiefly owing to the remarkable researches of Gaskell; but, in addition to the whole matter being so essentially *sub judice*, it is not for me to express any positive opinion upon it, and for further study I must refer you to the writings of that author. The reason why we are met with so much difficulty in this matter is because in all questions of tracing out homologies, we are always at a loss if we have not before us a series of ancestral forms wherewith to work out the stages of evolution that the nervous system has passed through. It is the loss of these intermediate forms which places us in this dilemma. Personally, I believe that anatomical research will do less than physiology towards settling these important and most difficult questions, and that, as a fact, we shall not advance very far towards their solution until we are able to approach them from the standpoint of their function, which of course is a totally different mode of comparative investigation. Perhaps I might indicate to you in a few words an instance of the difference in the amount that we have already learnt from anatomy and physiology respectively. Beginning with the highest apparatus which is likely to afford us the maximum

of differentiation, we found that in the crayfish the uppermost of the series of ganglia was clearly the one in which most initiation of movement started, but that that initiation was also shared by the second ganglion, and that between the two passed the gullet or œsophagus of the animal; whereas when we turn to the frog we find that the whole of the nervous system, which is capable not only of initiation but of the very simple property of reflex action, or simple muscular response to a peripheral stimulation, is permanently above (*dorsally*) the œsophagus or gullet, and nowhere is any part of it below (*ventrally*). Anatomically, therefore, one would not be justified in saying that the first two ganglia of the crayfish are comparable to the cerebral hemispheres of the frog; but if now we turn to physiology we find the physiological evidence to point directly to such a conclusion, and since physiology can show an agreement in function, and anatomy is not able to adduce absolute evidence either as to agreement or disagreement in the evolution of structure, it is likely that the physiological aspect of the case is the more correct one. Moreover, the brilliant investigations of Gaskell suggest that a perfect harmony underlies the apparently conflicting facts, and that the true homology lies between, not the gullet of the invertebrate and that

of the vertebrate, but rather between the gullet of the invertebrate and the central nerve canal of the vertebrate.

Putting aside all discussion of these recondite subjects, which are not immediately necessary to our present purpose, we will now examine the nervous system of a frog in further detail, and we shall find that anatomically we are introduced, in this animal, to an enlargement of the simple conditions which prevailed in the invertebrate. In the invertebrate we had to do with scattered and simple nerve centres which we called ganglia, and to and from which there ran nerve fibres. Now in the frog these ganglia, in which the reflex functions and their localisation are more concentrated, are built up together closely into the organs which we call respectively the brain, the little brain (or cerebellum), and the spinal cord. In Fig. 23 you see these parts represented. At *H.c*, &c., are the cerebral hemispheres, the optic lobe, the cerebellum, and the spinal cord (see also Fig. 24) You further note that, just as in the crayfish, each half of the body is supplied by half the nervous system ; in other words, that the nerve centres in the amalgamated brain and the spinal cord of the frog are just as much paired as the twin ganglia of the crayfish are. But herein enters a difference between the two animals. In the crayfish, the ganglia of the

FIG. 23.



Nervous system of frog viewed from the front.—*Ecker.*

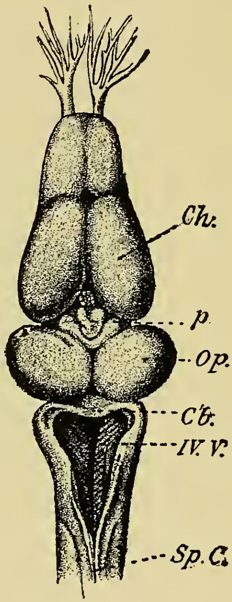
o = Eyeballs.
H.c. = Cerebral hemispheres.
I–X = Cranial nerves.
S = Sympathetic chain of ganglia and fibres.
S^1, S^2, *&c.* = Sympathetic ganglia.
M^1–M^{10} = Spinal nerves coming from cord.
M = Spinal cord.

one half of the body innervated the corresponding half and subserved its functions, therefore we say that the crayfish exhibits unilaterality of representation. From the frog upwards we are introduced to a new circumstance—viz., the fact that the sensory nerves, especially those of the eyes, have acquired a diagonal direction of growth, so that, as you see, the optic nerves absolutely cross one another (Fig. 23, II.), the result being that the eye of one side is in relation with the half of the brain that belongs to the other, and that this crossing on the sensory side is made up on the motor by a similar intersection of the channels, so that the muscles of one half of the body are able to work harmoniously in relation with the sense organs of that side. But this harmony is only maintained by means of these crossings of the channels. We cannot dwell upon the relations of the brain in this animal, inasmuch as that will form part of next year's course; we must therefore turn our attention to the spinal cord.

In looking at the spinal cord as it is shown in Fig. 25, it is obvious that it is divided by a median groove into two equal parts, and that it is a columnar structure, which terminates below in a point, but above passes into the brain. If we were to make a cross section of it we should find, as I stated in my first lecture, that it is tunnelled in its

centre by a minute canal, which passes upwards into the ventricle of the brain. Now, as a matter of fact, before it reaches the centre of the hemispheres, this canal widens out on the posterior surface at the upper part of the spinal cord just below the cerebellum, and here forms a lozenge-shaped space, which is known as the fourth ventricle (Fig. 24). The upper part of the spinal cord, which is thus hollowed out posteriorly, is that part which has received the name of medulla oblongata or bulb, and because it gives origin to the important nerves which regulate the action of the heart and the breathing, it has been looked upon as a special part of the central nervous system. For the present, however, we shall disregard this region and confine ourselves for the next few lectures to an examination of the functions of the rest of the spinal cord. You notice further (in Fig. 1 and Fig. 42) that

FIG. 24.



Brain of frog and upper part of spinal cord.—*Ecker.*

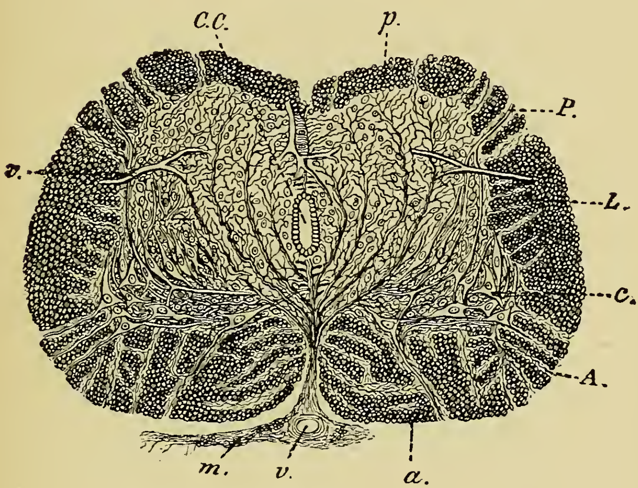
Ch = Cerebral hemispheres.
p = Pineal gland.
Cb = Cerebellum.
Sp. C = Spinal cord.
IV. V. = Fourth ventricle.
Op. = Optic lobe.

in the higher mammals the spinal cord presents a distinct enlargement where the nerves of the upper and lower limb are respectively given off. This, however, is far more marked in the higher animals; such, for example, as the bird and the carnivora. These swellings are spoken of as the cervical enlargement and lumbar enlargement respectively; the first being situated in the neck region, and giving rise to the nerves of the upper limb; the second being at the lower extremity of the cord, and furnishing the nerves for the lower limb. They are due to the greater development of nerve cells and centres, as well as to the addition of fibres, the increase in each case being related to the requirements of the limbs. We must now proceed to examine the anatomy of the cord more minutely; it practically has the same structure throughout, although the proportions of its constituents necessarily vary according to the amount of function the particular part may have to perform. It is always best to look at structure in relation to function, and I shall therefore describe its arrangement from the two points of view: firstly, the spinal cord as a conductor; and, secondly, the spinal cord as a nerve centre.

These two points of view are especially evidenced by a cross section of the organ (Fig. 25); you see then

that an immense mass of it is made up of nerve fibres; but there are other parts of it which have a greyish appearance, and in which are more especially grouped together the nerve corpuscles. The bundles of nerve

FIG. 25.



Cross section of the spinal cord of the frog.—*Ecker.*

C.C = Central canal.
p = Posterior column.
P = Posterior root.
a = Anterior column.
L = Lateral column.
A = Anterior roots.
c = Nerve corpuscles of anterior cornu.
v = Blood vessel.

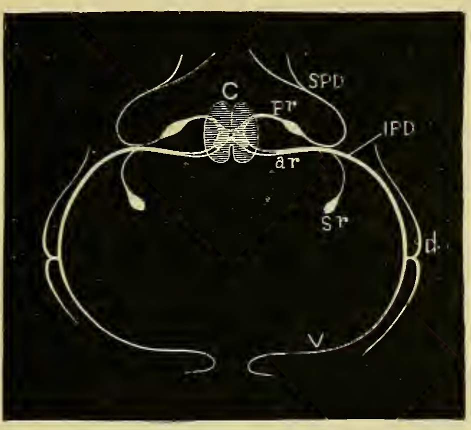
fibres are, of course, the structures we are now particularly considering. They are seen to be naturally grouped into definite regions of the cord, and separated from one another by the nerve centres before alluded to. Thus they are for convenience

spoken of as the posterior column (*p*), the lateral column (*L*), and the anterior column (*a*) on each side. It would be strictly more correct to call the posterior column the dorsal, and the anterior column the ventral in each case; but custom has so connected the terms anterior and posterior with the divisions of the cord in man, that it has usually been found more convenient to transfer the same nomenclature to the lower animals. The nerve fibres, which make up the columns, differ in size, but the significance of this is as yet imperfectly understood.

Turning now to the cord as a nerve centre, you find that the grey matter or part of the cord, which has very much the shape of the letter H (see rather Fig. 27), is that portion of it which contains the ganglion cells, and which consequently performs the functions of the cord as a distinct organ. These ganglion cells are arranged in two main divisions: those in the anterior or ventral part of the grey substance, which are large massive cells; those in the posterior part, which are small, and have evidently to do with the reception of impressions, the large ones subserving the functions of motor or efferent impulses. The cross-piece of the H is made up of nerve fibres which pass over from one side of the spinal cord to the other, and which are therefore supposed to have a commissural character.

It will now be convenient to review the connection of the peripheral nerves with the cord. You are already familiar with the fact that, opposite to the space between each pair of vertebræ of the spinal column, a nerve passes out into the body; and

FIG. 26.



C = Spinal cord cut across.
Pr = Posterior root.
ar = Anterior root.
SPD, *IPD* = Branches of compound nerve.
Sr = Sympathetic ganglion
v = Ventral termination of nerve.

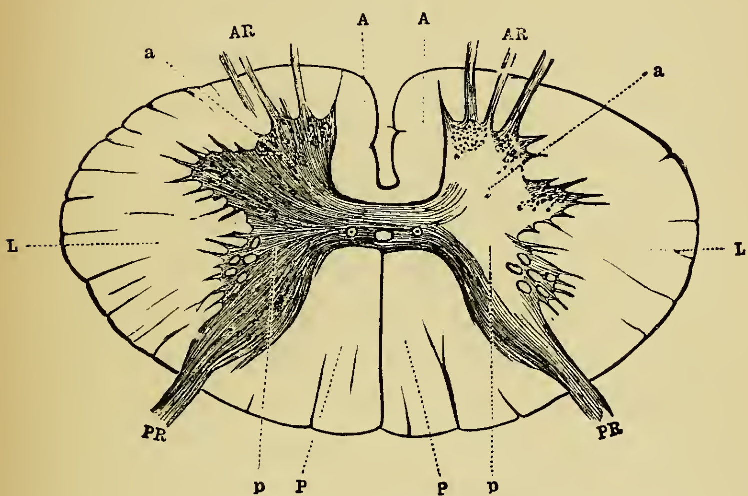
furthermore, that it arises from the spinal cord by two roots, an anterior root and a posterior root (Fig. 26). Fortunately, we are able to say that a good deal is known of the connection of these roots with the spinal cord. It will however, be better, I think, to say the few words I

have to say upon the particular points in the structure of the spinal cord of the bird and the cat, before discussing this connection, since it has been much more elucidated by investigation of the higher than of the lower vertebrates. The spinal cord of the bird requires no special description. The canal which penetrates it, however, opens at the lowest part in the lumbar enlargement, just like the fourth ventricle in the highest part, or medulla oblongata. This lower opening is known as the rhomboidal sinus.

Similarly, the spinal cord of the cat (see Fig. 1), as an example of general plan of structure in the carnivora, is merely a multiplication of the simple forms, and, consequently, when we examine the cord in the carnivorous animal, we only see a more complex arrangement of fibres and cells than what we discover in the frog. This complication does become of interest and importance, however, when we finally explain the arrangement of the spinal cord as we see it in man; but we must first turn again, putting that aside, to the condition of affairs in the frog. We do not know absolutely the course of the fibres as they enter the frog's cord by a sensitive or afferent channel, and we can only suppose that they are partly direct, partly indirect. We do know, however, that the nerve cells or

corpuscles of the anterior columns of grey matter are definitely connected anatomically with the nerve fibres of the anterior root or efferent channel.

FIG. 27.



Spinal cord cut across (man).

A = Anterior column.
P = Posterior column.
L = Lateral column.
p = Posterior part of grey matter (nerve centres).
a = Anterior or efferent part of nerve centres.
AR = Anterior roots.
PR = Posterior roots.

Consequently, if an impression travels up the posterior root or afferent channel and gains the spinal cord in the frog, it will reach the grey matter on the side where the small corpuscles are collected; it then passes across apparently an area

of obstruction, and enters the so-called motor cells, finally leaving them by the large nerve fibres which make up the anterior root. The same description also applies to the bird, and the chief interest attaching to it is the remarkable development of this simple nerve mechanism, and consequently, as we shall see later, great (so-called) power of recuperation of function in these animals.

In turning to the structure and functions of the spinal cord in the higher carnivora and in man, it is interesting to find that the actual performance of function in this species is subserved by a similar arrangement of nerve cells and nerve fibres, and that impressions come to the spinal cord by means of the posterior root, and appear to pass across from the small cells in the posterior part of the cord to larger cells in the anterior part, and out by the anterior roots. So that, as we shall see directly in subsequent lectures, in whatever vertebrate animal we take, this mechanism provides for response by movement in answer to a single sensory stimulus, in exactly the same way as occurs in the medusæ as well as in other invertebrates. At this point, however, I ought to indicate to you, especially as this is only a prefatory account, that the nerve centres in the spinal cord are arranged in groups according to the work which they have to perform, and that there are, in

the carnivora, numerous collections of such nerve centres corresponding to each segment of the cord —that is to say, each district of the cord which is in relation with the two roots of each single nerve. The activity of the spinal cord in the higher animals has to be considered in regard to the functions of the viscera, since it is not necessary for the correct performance of most of these that the brain should be intact, the spinal cord being quite equal to the task of providing for their being successfully carried out. But it does so by means of groups of nerve cells, which are aggregated into convenient places. Hence, when we are able to leave general principles and come down to details, we shall see that there are collections of such nerve centres in the upper portion of the spinal cord or bulb for the movements of the heart and lungs, as well as in part for those of the alimentary canal. Besides these, there is, in addition, a most important central mechanism situated here, which regulates the size of the blood-vessels all over the body. This last apparatus attains its purpose by operating upon centres lower down in each segment of the spinal cord, each, moreover, being situated opposite to the origin of every nerve. Then, in addition, we have other centres aggregated in the lower part of the cervical enlargement, the upper

part of the dorsal cord and the lumbar enlargement more especially, which regulate entirely the movements of the viscera, their successful performance of the functions they subserve, and moreover the state of the circulation within them. So much is this recognised, that it is customary to speak of these last-named centres more particularly as the "lumbar centres."

I have now spoken so far of the cord as a conductor of the sensory impulses upwards, and of its being an organ in which nerve centres are conveniently grouped together for the performance of definite acts. I have said nothing about it as a conductor downwards of impulses coming from the brain. The fibres of the spinal cord which carry out this purpose run in the lateral columns in a small bundle towards the posterior side of the column, and all the evidence goes to show that they terminate in the nerve centres *seriatim* down the cord. In man and the highest apes this duty is imperfectly shared by the anterior column as low as the middle of the dorsal region, and probably lower (*Tooth*).

Proceeding to the next point or general principle, we have to consider how far in these vertebrata the nerve centres, thus congregated in the spinal cord, are connected with one another, just as we saw the nerve centres or ganglia in the invertebrata to be

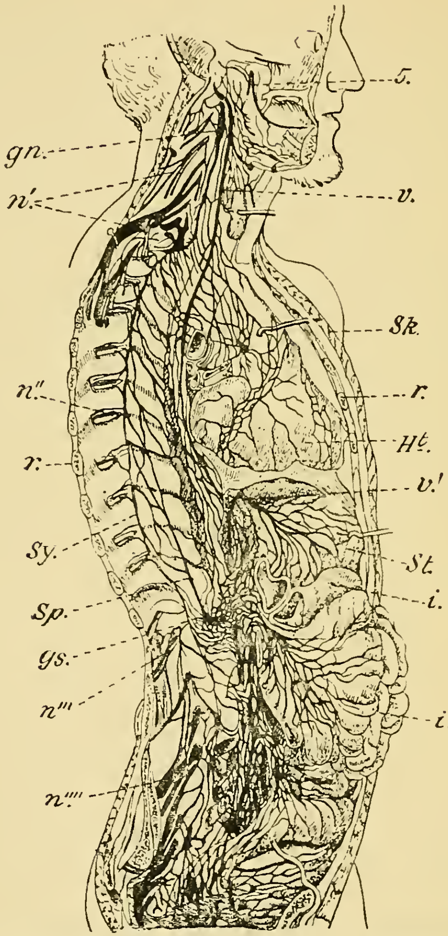
connected by commissures. In the crayfish you saw that the ganglia were united by longitudinal bundles of nerve fibres, and crosswise also by little transverse ones. In the higher animals, where the cord, as you see, is such a wilderness of fibres and cells, it is not easy to speak so very definitely on the union of the centres one with another. We are therefore obliged to draw evidence on the point rather from physiology than anatomy. Physiology teaches us the following considerations: In the first place, each half of the spinal cord is in relation with its own half of the body, so that, as far as it goes, each half of the spinal cord represents a single chain of ganglia running down one side of the middle line in the crayfish. But whereas the physiological experiments on the crayfish went to show that in that animal there was no possibility of one chain of ganglia supplementing the other, this is not quite true of the higher forms, inasmuch as in them, the destruction of the centres on one side of the cord is so provided against by commissures and cross junction lines, as to render it relatively easy for a nerve impulse to pass across, so that if its usual route were interrupted it could nevertheless reach the muscles. It is not to be imagined, however, that this supplementary action is developed in the

higher animals as a constant feature, as this possible supplementation of function is only to be obtained by exercise after injury has befallen the organ. To sum up, therefore, unilaterality of representation prevails, but there is a possibility of a certain degree of bilaterality becoming developed.

LECTURE V.

You will now have grasped the salient fact that the spinal cord throughout the vertebrata acts as a conductor of impulses *to* the brain, which we call sensory, or, better, *afferent;* and also *from* the brain, these being commonly termed motor, more properly *efferent;* while in addition the grey matter of the spinal cord acts as a centre for the discharge of simple functions, such as movement, &c. I now have to go further, and to point out to you that besides this system of ganglionic centres and nerve fibres, there are additional ganglia in connection with the nerves that enter and leave the spinal cord. The first and most obvious of these is the ganglion which is seated on the posterior root of each spinal nerve, and which I showed you in the last lecture (Fig. 26). The second is a system of ganglia which are united together apparently by a chain of fibres linking them in exactly the same way as the ganglia in the crayfish are connected (Figs. 23, 28). These form what is called the sympathetic system or

FIG. 28.



Dissection of the trunk laid open from the side. Altered from Hirschfeld and Leveillé. Nerves shown black.

Sy = Sympathetic chain.
Sp = Splanchnic branches of the same.
n' = Cervical spinal nerves.
n'' = Dorsal spinal nerves.
n''' = Lumbar spinal nerves.
n'''' = Sacral spinal nerves.
v = Vagus nerve, tenth cranial.
5 = Fifth cranial nerve.
r = Ribs cut across.
v' = Vagus supplying stomach. (*St*).
gn = Uppermost sympathetic ganglion.
Sk = Skin and fat.
Ht = Heart.
gs = Solar plexus.
i = Intestine.

chain, because it was formerly believed by the old anatomists that this system of ganglia in a chain had for its function the duty of bringing the various organs in the body into harmonious correlation, and they built upon this theory a whole pathology or explanation of diseases, which reached its acme at the beginning of the century in the teaching of Abernethy, but which, like all theories not founded on experiment, has already become extinct. We know now that these ganglia have a distinct relation to certain fibres which leave the spinal cord and which are distributed to the blood-vessels and to the viscera. As regards the gross position of these ganglia, you will see that the chain stops high up, at the base of the brain in the skull, the branches coming into connection with the efferent cranial nerves, and that it then runs down the neck, thorax, and abdomen, receiving fibres from the spinal cord and giving off fibres to various organs. It is my purpose to-day to speak at length on this great sympathetic system, so that we may dismiss it and reserve our time for the discussion of infinitely more important parts of the spinal cord and the bulb, to which indeed the sympathetic system is but an appendage.

As you saw shown in the frog, in Fig. 23 and in Fig. 32, taken from Gaskell's work on the dog, the sympathetic chain appears to start in the little ganglia

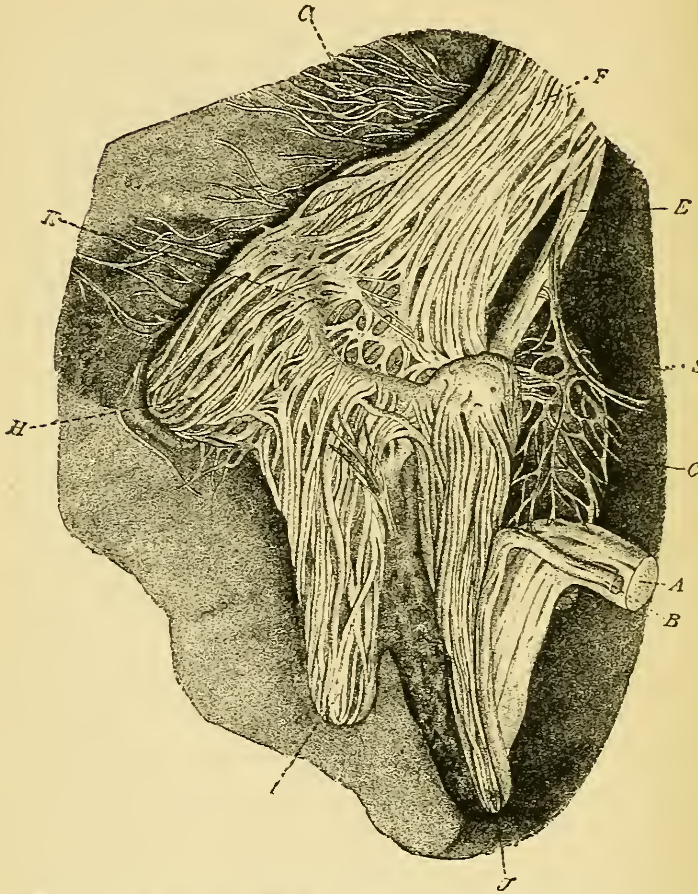
in connection with the third and fifth cranial nerves. You further notice issuing from the spinal cord the anterior and posterior roots already described of each spinal nerve, and that some of these are represented black in contrast to others white. Those coloured black include the small medullated fibres I described in the last lecture, and most of these, after they have come into contact with the sympathetic ganglia, lose their medullary insulating sheath, so that from the ganglion they issue as series of branches of non-medullated nerves. Yet further, you see that some of the branches coloured black escape, as it were, the sympathetic ganglia, and run forward to other ganglia which are nearer the viscera to which they will subsequently furnish fibres. In these distal ganglia they finally lose their medullated sheath. Consequently we find that all the viscera of the body are innervated by nerve fibres which leave the spinal cord, and enter into the composition of ganglia which have the duty of furnishing branches of nerves to the various organs. Thus it matters very little whether the ganglia happen as it were for convenience to be arranged in a chain along the spinal column, or whether they are situated around the blood-vessels which enter into the various organs, and hence it is that their mere morphological arrangement is more

a matter of general interest than a revelation of function. It now remains for us to consider in further detail their structure and function. As regards the structure, that differs according as to whether we are speaking of the little ganglion on the posterior root of each spinal nerve, or of one of the ganglia which forms part of the so-called sympathetic system. It will perhaps be more convenient to deal first with the former of these.

Structure of the Spinal Ganglion on Posterior Root.

The nerve fibres that run up a nerve and, arranged in bundles (see Fig. 29), enter into the composition of the posterior root, are medullated nerve fibres; they run through the ganglion, and, with very few exceptions, enter into conjunction with the ganglion cells. Now this conjunction with nerve cells in the spinal root ganglia is very interesting and curious. We have seen that in the lower animals a nerve fibre entered a ganglion cell and left it by one or more branches. But with the ganglion cell in the posterior root of higher vertebrated animals it is quite otherwise; in this case the nerve fibre runs through the ganglion and gives off a branch at right angles to its course, this branch

FIG. 29.

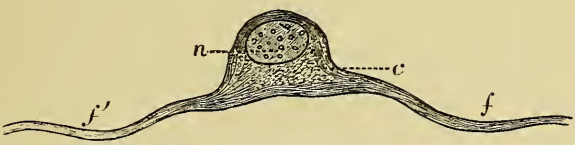


Marginal view of the Gasserian ganglion on the fifth cranial nerve.—*Bourgery and Jacob.*

A = Third cranial nerve.
B = Fourth „ „
C = Carotid artery with sympathetic plexus upon it.
S = Sympathetic nerve plexus on carotid.
E = Sixth cranial nerve.
F = Trunk of fifth nerve, sensory root.
G = Branches supplying the dura mater.
H, *I*, *J* } The three divisions of the nerve.
K = Substance of ganglion. Situation of nerve corpuscles.

passing into a nerve cell in which it terminates. This arrangement is commonly spoken of as a T-shaped junction, and is an anatomical structure of much interest, for it is very difficult for us with our present views of nerve function to understand what it means; whether there is some distinct storing up in the nerve cell of nerve impulses, or whether, as du Bois Reymond originally suggested, the nerve cell under these circumstances acts like

FIG. 30. (*His.*)



an electrical relay. This peculiar relation of a nerve cell to the side of a nerve fibre belongs, so far as we are aware, only to this special system of ganglia, but its importance is shown by the researches of His, who discovered that in its development the nerve cell appeared as a local swelling on the side of the fibre, as is shown in Fig. 30, which is from a photograph of one of His's drawings. The structure therefore of a spinal ganglion—that is, the ganglion on the root of every nerve—is something quite special, and deserves to be considered apart.

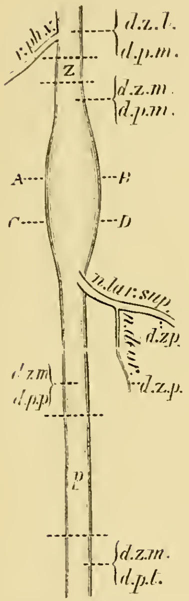
Function of the Spinal Ganglion on the Posterior Root of a Spinal Nerve.

Of the actual function of this remarkable arrangement of nerve cells on the posterior roots of the spinal nerves, I cannot, unfortunately, tell you much, although a certain amount of physiological research has been expended on this very question. The investigations of du Bois Reymond, who employed the method he had discovered, and which I mentioned to you in the last lecture—viz., that of finding out, whether a nerve impulse was or was not passing along a nerve fibre, by means of noting the presence or absence respectively of the electrical change which he had previously found always to accompany such passages of impulses—led him to test the spinal ganglion by the following means. Du Bois Reymond observed that if he excited a nerve root above the ganglion, as shown in the accompanying diagram (Fig. 31), and connected the lower end of the nerve with the galvanometer, that the latter instrument revealed the existence of the excitatory change in the part of the nerve beyond the ganglia; the impulse must, therefore, have passed backwards through the ganglion. The next important observation was made by Exner, who discovered by means of a particular method which I need not describe to you, as it would take

more time than the point is worth, that apparently this passage of the nerve impulse was not attended by any extra loss of time, such as might have been expected to follow had the impulse first to leave the nerve fibre, then pass into a nerve cell, and out again into a nerve fibre. It is possible, however, that Exner's method only revealed the fact that the artificial excitation of the nerve fibres was propagated directly along the protoplasmic axis in the direct line of the nerve, and that it did not reveal what went on in the little T-shaped branches that went off from the nerve cells or in the nerve cells themselves. That this is more than likely is shown by the investigations of Gad and Joseph, who discovered that in the system of peripheral ganglia there is a distinct loss of time as the impulses pass through. They arrived at this conclusion by experimenting on the vagus nerve in the rabbit. The vagus nerve in this animal exhibits a large ganglion soon after it leaves the medulla oblongata. That part of the spinal cord is, as already suggested, connected with various important functions of the body—viz, the action of the heart and respiration. For the present we are concerned only with the latter. When the central—*i.e.*, the upper or brain end of the vagus nerve—is stimulated, it is found that the breathing is immediately altered.

The period of time which intervenes between this centripetal excitation, and the production of the effect, is the total amount expended in the passage of the excitatory condition or impulse to the centre in the medulla and down to the respiratory muscles. By eliminating the period lost in mere conduction in the fibres, and by applying the excitation first on the distal side of the ganglion and then on the proximal (at p and Z respectively) it was easy to find the difference in time, and this difference these authors found to be about $\frac{3}{1000}$ sec. This loss of time, however, cannot be accepted as finally deciding the point, inasmuch as several side issues make it difficult to determine the exact influence of the excitation (Fig. 31). There remains now only one further point concerning the functions of these ganglia, and about which we are in no doubt. It is a most important function, and one which we shall see is exercised to

FIG. 31.



Vagus ganglion in the rabbit.—*Gad and Joseph.*

The upper end of the figure is the central end of the nerve; consequently all impulses aroused by exciting the nerve at p must pass through the ganglion, which is the swelling on the trunk.

an enormous extent by the nerve cells of the spinal cord. This is the duty of maintaining the nutrition of the nerve fibres with which the ganglion is in connection. If, for instance, the nerve root be divided on the spinal cord side of the ganglion, it is found that almost all the nerve fibres which pass into the spinal cord degenerate and waste away simply because they are no longer in connection with the ganglion cells. Now it is very difficult for us to imagine what the nature of this influence which the ganglion cell exerts upon the nerve fibres can possibly be, but the fact remains, and we may perhaps more profitably postpone its discussion until we shall subsequently see its greater development in the spinal cord.

Structure and Arrangement of the Ganglia of the Sympathetic System.

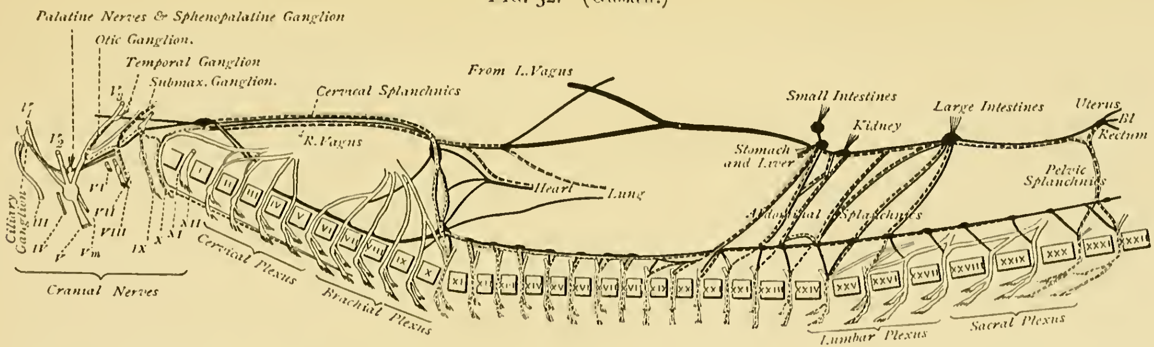
I cannot give you all the details—that is, enumerate to you all the branches and nerve centres in the sympathetic system—that would be beyond the scope of this present course; and, moreover, the fact can be easily learned by reference to any text-book on anatomy; but I want to emphasise a few general points which we owe to the keen insight of Gaskell. The first is that every spinal nerve

practically may be considered to arise, whether from the base of the brain or from the spinal cord, by two sets of fibres, not merely arranged in anterior and posterior roots, as they appear to the naked eye, but somatic and splanchnic; or, in other words, supplying the body structures—*i.e.*, bones, muscles, skin, &c.—on the one hand; and the viscera—*i.e.*, heart and blood-vessels, alimentary canal, &c.—on the other; further, that where the splanchnic function has to be subserved, there the fibres which leave the spinal cord must pass through a peripheral ganglion, as I have already stated. The situation of these peripheral ganglia under this view therefore becomes a point of great interest, and we find that they are grouped together and in such proportion as will provide for the concomitant number and size of the viscera to be supplied. Thus, while in the neck there is no passing out of fibres from the spinal cord to join the so-called sympathetic system, to be found to any great extent, there is an outflow of such fibres above through some of the cranial nerves, and most especially naturally the nerve which we call the vagus, and which passes down through the body to innervate the most important viscera, not only those of the heart and lungs, but also even the liver, stomach, &c. Intermediately in the neck, where there are no viscera except the air tube or trachea,

the food tube or gullet, and main trunk blood-vessels, it is easy to understand, according to the views we have just enunciated, why these fibres should be in insignificant proportion; whereas, as soon as we come opposite the thoracic portion of the spinal cord, more of these fibres pour out to supply both the various organs according to their proximity, and distal parts as well. In this diagram (Fig. 32), we see all these points illustrated very clearly, and the relative development of these nerves and ganglia. Although it is not possible to describe the special nerve supply of all the different viscera or organs of the body, still I wish to allude to that of the heart and blood-vessels, inasmuch as not only has the relation of the action of the heart to disturbance of the nervous system always attracted attention from the time of Plato, but because of recent years much has been accomplished scientifically in advancing our knowledge in this direction.

Since the immense discovery by Claude Bernard of the so-called vaso-motor system of nerves—that is to say, the arrangement of nerve fibres which controls the calibre of the blood-vessels—to recent time, when Gaskell especially has added to the facts which explain how changes in the beat of the heart can be induced, there has always been a large field for

FIG. 32. (*Gaskell.*)

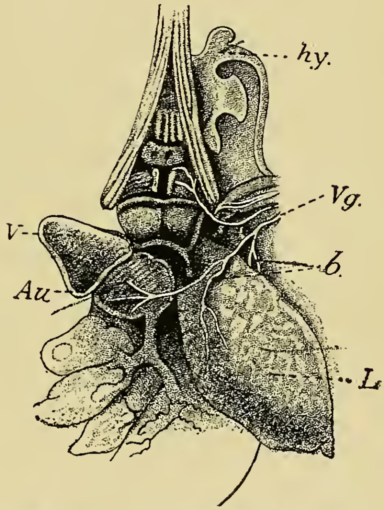


The square blocks with the Roman figures represent the vertebræ of the spine. The spinal cord is not shown; but the roots arising from it are indicated, two for each intervertebral nerve.

The visceral nerve fibres—*e.g.*, to the vessels, &c.—are indicated by the dotted lines, and the roots by which they leave the spinal cord are thus made clear.

further exploration open. It is my purpose, however, only to touch upon one point, to illustrate to you more completely, what influence the nervous system exerts upon the blood circulatory apparatus. The vagus nerve, of which I spoke just now as acting as the medium of impulses which leave the medulla and influence the heart-beat, is the example I choose. In the frog it is easy to observe this, since we can in the anæsthetised animal remove the cerebral hemispheres, so that it can unquestionably have no consciousness of pain. If then the heart be exposed and gently raised, as shown in the drawing (Fig. 33), the vagus nerve running down to supply it is also visible, and the special branch of it which ramifies over the base and side of the organ to reach little peripheral ganglia in the substance of

FIG. 33.



The distribution of the vagus nerve to the heart and lung.—*Ecker*.

hy = Hyoid bone.
V = Ventricle of heart.
Au = Auricle of heart.
Vg = Vagus nerve.
b = Branches to lung, &c.
L = The lung.

the heart muscles. If we now apply an electrical current to the vagus nerve to excite it, we find that it exerts a marvellous effect on the heart-beat, slowing it, and even arresting it altogether, as you see, and as is shown also by causing the thread, holding the end of the heart, to move a lever, which writes by a point on a smoke-blackened moving surface so that we obtain a record defining the moment when the heart's movements are arrested. Similarly it can be shown that the medulla oblongata is the station *par excellence* for the impulses which alter the calibre of the blood-vessels and cause them to contract (pallor), or to dilate (flush). These vascular nerve impulses pass down the cord and out by the roots of the spinal nerves, to be distributed with the peripheral branches of the sympathetic system so called.

These two examples will suffice to illustrate the existence of nerves which govern the organs and blood-vessels of the body. We are now in a position to discuss the minuter structure of this great sympathetic system, as it is called, and later to briefly examine the experimental results by means of which its function has been elucidated.

Minute Structure of the Ganglia of the Sympathetic System.

The structure of one of these peripheral ganglia, or sympathetic ganglia, is very different from that of the spinal ganglion just described. As you see in the beautiful drawings by Key and Retzius, the nerve cells of a sympathetic ganglion are not in connection with the nerve fibres by T-shaped branches of the latter, but, on the contrary, they are many branched, or, as we more commonly term them, multipolar, and of these numerous branches, no doubt one or more are in connection with the nerve fibres, while the others for aught we know are in more or less intimate connection with their neighbours in the ganglion. You thus see at once that in one of these peripheral ganglia, the condition of affairs is quite different from that which prevails in the ganglion of the posterior root of a spinal nerve; in that case we had a through nerve path, upon the channel of which the nerve cell was, as it were, simply superadded; whereas in the present case the nerve fibres appear to terminate in the nerve cell, from which other fibres take origin, but in what way does not appear quite definite. Putting it in another way, in the case of the peripheral or sympathetic ganglion, there appears to be

a structural block in the course of the nerve fibre, by reason of the interposition of a cell, whereas in a spinal ganglion the cell is not situated in the main line as it were, but on a branch line. The physiology of these ganglia, which we shall now consider, tells exactly the same story. I have already alluded to the observations of Gad and Joseph, which show that the peripheral ganglion on the vagus in the rabbit is a distinct seat of delay to impulses ascending that nerve and ultimately affecting the respiratory centre. This delay is very interesting, and very valuable work, but of a different kind, has been done upon these ganglia in this country by Messrs. Langley and Dickinson. These authors discovered that if a solution of nicotin be taken (and as weak a solution as 1 per cent. suffices), this very powerful nerve poison acts quite differently upon the elements which compose the ganglia; thus, for example, it at first paralyses the nerve cells, but leaves the nerve fibres unaffected. This very remarkable discovery was brought about in the following way. Among the many duties which the nerves that leave the spinal cord and enter these peripheral ganglia have to perform, there is one which is very easy of observation, and therefore extremely useful as an index. I refer to dilatation of the pupil of the eye. If, in an animal that

has been rendered unconscious with chloroform or ether, the neck portion of the sympathetic chain below the chief ganglion (the superior) be exposed, and then stimulated with an electric current, it is found that the pupil, which is supplied by the branches of this portion of the system, actively dilates; whereas if the ganglion into which the chain of fibres passes, be painted, even once only, with the solution of nicotin, excitation of the nerve does not produce the slightest effect. That it is the specific action of the poison upon the nerve cells and not upon the nerve fibres, is shown by the further discovery of these gentlemen that the nerve fibres will endure being painted with a nicotin solution without this interfering with their conductivity. The employment of this method has enabled these writers to discover what hitherto was absolutely unknown, and what indeed there was no immediate likelihood that it should be known, and this was that the block which I have just spoken of does actually occur in a peripheral ganglion. Thus, for example, there are fibres the excitation of which prevents movements of the stomach and allied organs, and the fact that the application of nicotin to the ganglion entirely abolishes this function, and that it does not interfere with the conductivity of nerve fibres, shows us that the nerve cells of the peripheral

ganglia (in this case of the solar plexus, see Fig. 28) are places in which the nerve fibre absolutely stops, and that the nerve cell is capable of supplementing, or even greatly altering, the original impulses which may have left the spinal cord.

Finally, there is a point, which I have already mentioned, that is entirely in harmony with these observations. You will doubtless remember that in the last lecture I described to you how that the nerve fibres which left the spinal cord, and ultimately ran into these peripheral ganglia of the so-called sympathetic system, after they had entered the ganglion, in each case lost their insulating sheath. This anatomical fact suggests most strongly that the medullated fibre terminates its course in the nerve cell.

I now come to another division of the function of this so-called sympathetic, but simply peripheral system, which is a very interesting question physiologically, but upon which extremely little research has been expended, although it would make a good field for further investigation—I refer to the conduction of *afferent*—*i.e.*, so-called sensory—impulses from the viscera through these nerve fibres and peripheral ganglia. We are all aware that under ordinary circumstances—that is to say, of health—we are not conscious of what is going on, to use a

popular phrase, inside us, but that as soon as the parts become hyper-sensitive by reason of being inflamed or injured, then we are conscious of what we call pain. Even then the important principle of localisation does not come into play. We are only very vaguely aware of the position of the part that is in trouble, and very often this information is only gained in consequence of some portion of the body wall being also affected, and by this means somatic as well as splanchnic nerves being excited. It is a tempting subject to speculate upon, this very remarkable absence of afferent impressions in general, and especially of localised afferent impressions, from the viscera, and to bring that point into relation with the anatomical fact of the nerve fibres supplying these parts being deprived of the medullary or insulating sheath. It is conceivable that nerve energy, like other forms of physical energy, may depend for its more perfect conduction on physical conditions similar to those which determine or not the correct transmission of electrical force. However that may be, the truth remains that the brain, in the highest animals, does not receive sufficient afferent impressions from these peripheral ganglia to enable it to form any conscious idea of what is passing in the structures beyond. I particularly mentioned the highest animals, because we must be very cautious upon this point as regards

the lower genera, even the carnivora, since in them we find that, over a considerable extent of the folds of membrane which support the abdominal viscera, the most highly organised nerve-endings and fibres exist, such as are found in the most sensitive parts of the fingers. It would seem therefore that these animals have thus a distinct mechanism for the appreciation at least of the position of the viscera, though whether that appreciation is actually a conscious perception or even recept—that is to say, whether the cortex of the cerebral hemispheres is aroused or not—we are quite unable to express any opinion, or whether indeed it may not be that the impulses pass no higher than the simple reflex centres in the spinal cord.

To sum up the use and meaning of the sympathetic system and series of ganglia. We see that, although apparently separated from the central nervous system, it is only a specially arranged portion of the peripheral distribution of the nerve fibres branching from the brain and spinal cord, and further that its ganglia are but peripheral stations on these fibres.

It is certain, of course, that impulses are constantly ascending from the viscera along these channels to gain the nerve centres, and therein set up responsive or reflex processes which issue

forth especially from the cord, and the effect of these is movement—*i.e.*, contraction or dilatation of the organ or of the blood-vessels within it.

I intend next to describe the general functions of nerve cells and fibres when these are in an excitatory condition, inasmuch as it is impossible otherwise to grasp fully the connection between function and structure, such as it is the object of these lectures to demonstrate, in the spinal cord and ultimately in the brain.

To effect this object we shall be quite justified in proceeding to speak generally of the functions both of nerve fibres and of nerve cells, while using as our illustrations the simple tissues of the frog for the most part, because not only are these the more easily treated and examined in the living state without inconvenience, but also because in their essentials (principles, see Lect. IV., commencement) the phenomena they exhibit do not differ from those produced by the same tissues of higher animals.

However simple it might appear, the task I am now setting myself is not an easy one; for we have not the precise knowledge of nerve energy which is really requisite for the purposes of differentiation of function.

In fact, as regards nerve energy itself, we have

scarcely advanced beyond the theoretical position taken up by Newton two hundred years ago, and which I quoted to you—viz., that it exists in the form of vibrations affecting the molecular structure of the protoplasmic core of nerve fibres. We have, in fact, only proceeded as far as the determination of two facts, to which also I have already alluded—viz.:

(1) The rate of transmission of such vibration.

(2) The electrical change which is the accompaniment of such transmission.

There are, however, certain general physiological laws upon the subject which are well understood, and which condition the functional activity of nerve centres and fibres. We shall therefore, with additional advantage, combine together the consideration of all these points.

LECTURE VI.

Having reviewed the general arrangement and relations of the spinal cord and ganglia, and having seen that the spinal cord acts as a conductor of nerve impulses as well as an originator of them, in obedience to certain definite laws; and having seen, further, that the apparatus which fulfils this latter function is ganglionic structure situated in the substance of the cord around the central canal, we cannot dwell further on its minute arrangement without discussing in considerable detail certain general principles which underlie the functional activity of nerve fibres and nerve cells. Investigation of the structure of the spinal cord more especially, therefore, has been conducted on the two lines: (*a*) anatomical, (*b*) physiological. And while both methods are very fruitful in results, it is the latter of the two that has really furnished us with the most definite knowledge of the intricate action of the spinal centres, although frequently enough the information it gives us is very difficult

of interpretation, and may even appear contradictory.*

During the last three years a fresh method of investigation by Mr. Gotch and myself has, I hope, partly relieved us of this difficulty, and I wish to-day to explain to you the general application of this method, after we have seen the principles according to which the conduction in nerve fibre is carried on.

We will begin, therefore, with the conductivity of nerve fibres. Now the first point we have to remember is that the nerve fibre from the time of its complete development is a single strand of protoplasm, which may or may not be covered with an insulating or medullated sheath. This strand of protoplasm presents in the living condition, as well as after it has been variously treated so as to exhibit more clearly the details of its structure, a delicately fibrillated appearance, the fibrils running longitudinally. So far as we know the structure of the protoplasm, it is probably identical with that

* Upon the latter point—namely, the apparent contradiction of experimental results—I would only refer to what I said before—viz., that the great difficulty, especially in examining the spinal cord, is to differentiate between the functional activity of mere fibres as contrasted with that of nerve cells, the difficulty being also greatly increased by the latter structures communicating with the former. Any seeming contradiction arises from this cause, and will doubtless ultimately be satisfactorily explained.

of the protoplasm of lower kinds, with such even as that of the white blood corpuscles—namely, that it consists of a kind of firmer skeleton or framework, and a softer semi-fluid or viscous substance, which is contained in the meshes of the skeletal network. In the case of the nerve fibre, just as in the case of nerve cells, the skeletal framework may probably be the fibrillar structure before referred to. It is very interesting to see at any rate that the protoplasm of a nerve conductor has a distinctly longitudinal arrangement, which, it is not going too far to suggest, may, by virtue of this fact, be more adapted to the polarisation of its molecules for the better transmission of nerve impulses.

This being the nature of the structure, we will proceed to investigate the circumstances which more particularly condition its capability of conduction and its excitability, or, in other words, the ease with which it can be aroused. Various physical and chemical agencies improve its conducting power, or at any rate appear to do so; I make this latter reservation, because the exact interpretation of physiological experiment necessarily becomes to a certain degree modified by the advance of science and the accumulation of more experimental work; in short, therefore, by more knowledge of the subject. A good example of this is the experiment

upon the influence of heat, as I will now demonstrate before you. Warmth naturally is always conceived to be an encouragement to the functional activity of protoplasm, but it is not quite certain as to how far this simple interpretation of its influence is correct, or whether, in these particular experiments, the heat does not materially modify the resistance of the nerve tissue to the excitation. In this preparation you observe that the nerve passing into the muscle is laid upon two pieces of wire, or electrodes as we call them, which are connected with an induction coil that is served by a battery. When the current, thus obtained as a series of shocks from the induction coil, is thrown into the nerve, its strength can be so adjusted as to be inefficient to cause the muscle to contract—that is to say, it is what we call a subminimal stimulus, because the excitation is just unable to arouse the nerve sufficiently to cause an impulse to pass down to the muscle and make it contract. If now, however, while we are sending these ineffective shocks into the nerve, we bring near the latter a heated bar of metal, so that the radiation from the bar should gently warm the fibres, we see that the muscle instantly contracts, showing that owing to the heightened activity (? diminished resistance) of the nerve fibres, the stimulus which was before inadequate, is now equal to its task.

In the same way cold effects a converse influence* —namely, it diminishes the conducting power (? increases the resistance) of the nerve.

The next point respecting the conductivity of the nerve fibres is one the meaning of which is not yet fully understood, and which depends upon the anatomical relations of the fibres. Thus it has been shown that if we take the spinal nerves as they issue from the spinal cord, and if we test them at various points in their course, we shall find, as Heidenhain and Bernstein did, that they are more easily excited the nearer they are to the spinal cord—*i.e.*, to the nerve centres; and we shall see later that there is other evidence of the same thing —namely, an increased activity apparently of the nerve fibres the closer we are to their junctions with nerve cells.

Another mode in which the conductivity of nerve fibres is greatly influenced by external physical means, is that of sending a constant electrical current streaming along the protoplasm of the cores of the nerve fibres. This operation throws them into a state which is called electrotonus, and, according to the directions of the polarising current which is thus sent into the nerve, greatly

* Except in the special case of cold directly applied to a nerve trunk. *Cf.* Gotch: "Proceedings of the Physiological Society," 1891.

modifies its conductivity or excitability, favourably or unfavourably. So easily is this brought about, that if when one nerve is excited, and consequently its electrical condition altered, it be placed close alongside of another, it will induce the same condition of electrotonus in its neighbour, and so arouse nerve impulses in the second nerve, and cause any muscle in connection with it to contract. The most striking experiment which illustrates this remarkable fact, and which has proved useful in nerve physiology, was termed by its discoverer, du Bois Reymond, "secondary tetanus." The arrangement of the experiment is extremely simple. Placed horizontally, is a muscle with its nerve depending from it, then above this muscle is another similarly placed with its nerve also hanging downward, but laid upon the muscular substance of the first preparation. If now the first muscle be made to contract by stimulating its nerve, the second muscle will also immediately do so, because the electrotonic state of the first preparation has been communicated to the nerve of the second.

Lastly, as regards conduction, I need only add that, so far as we know, if a nerve impulse be generated in the middle of the course of a nerve fibre by suitably localised excitation, it travels both

ways along the nerve fibre—that is to say, up and down. This is very important, for although we have little doubt that as a rule impulses are in the habit of only ascending or descending nerve fibres, it is nevertheless quite clear that they can go either way in conductors if necessary. More than this we do not know, and it is a great pity that further investigation is hardly possible as yet, for it would be most interesting to ascertain whether a nerve fibre is capable, like a telegraph wire, of having sent along it simultaneously several different messages, provided suitable apparatus is present at each end for reception and transmission.

I now wish to pass on to the special consideration of the manner in which nerve fibres react to excitation, and the phenomena which they exhibit in the course of such reaction, and I will take the various ways in which they can be stimulated in their simplest order, although the most interesting by far is the last.

1. *Mechanical Excitation.*

If a nerve supplying a muscle be suddenly compressed, as you see, it evidently excites a nerve impulse, which is sufficient to cause the muscle to contract, and I may add it is also sufficient to cause the

phenomenon of an electrical change in the nerve fibre, to which I shall subsequently allude. As an instance of the physiological effect upon the entire body, of mechanical irritation of nerve fibres, it is sufficient for me to remind you that when the so-called "funny-bone," or ulnar nerve on the inner side of the point of the elbow, is pressed, we not only feel pain and discomfort at the point pressed upon, but we also refer the effects of the pressure to the tips of the fingers. This latter complication is simply due to an error of appreciation on the part of our nerve centres, and the whole process is a good illustration of the way in which nerve fibres can be irritated mechanically.

2. *Chemical Excitation.*

Various chemical reagents possess the power of more or less actively exciting nerve fibres; thus the immersion of the nerve in carbonate of potash or solution of glycerine is sufficient to cause the development of nerve impulses which produce contraction of the muscle in connection. While possibly the action of these chemical substances may be partly specific, it is nevertheless probable that it is also, and perhaps in the main, due to the abstraction of water from the fibres.

3. *Thermal Excitation.*

So also heat when suddenly applied to nerve fibres will* stimulate them into action.

4. *Electrical Excitation.*

Of all means that have yielded information on this question none has been so rich in results as the electrical method of stimulation. In the first place, we learn at once, by employing different forms of the electrical current, that nerve fibres do not react always in the same way to stimuli, and that these, to be effective in influencing the nerve fibre, must be of a certain degree of intensity; thus, for instance, with a mechanical excitation, very slow and prolonged pressure does not excite nerve fibres, it is necessary that it should be rather sudden in its application: so it is with the electrical current. We can take, as you see before you, such a powerful current as is derived from two Grove's cells, and when by means of this key, which is a convenient method of gradually letting into the nerve the stimulus, we apply it to the nerve fibre, it is obvious that, so long as we turn the key slowly, the

* There are exceptions to this rule as far as sensory impressions go. *Vide* "Journal of Physiology."

nerve fibre is not stimulated, and the muscle does not contract; whereas if the key be turned sharply so as to increase suddenly the strength of the current running through the nerve, the nerve impulse is aroused, and the muscle instantly responds to it. Direct observation has been made upon this point, and the most efficient period during which the closure of the current acts has been determined by various observers, and notably by Hermann, who found that it was about $\frac{2}{100}$ of a second. Du Bois Reymond had previously shown that if the constant current were applied without variation a relatively enormous difference of potential was necessary to evoke tetanus, and that its application produced after-effects. It is not clear whether this mode of action of the current is not partly due to electrolytic changes in the nerve fibres, or whether it is a true physiological influence.

This property of the constant current in inducing electrolytic changes in the nerve fibres constitutes, of course, a serious disadvantage to its employment in physiological experiment, and, moreover, it is inconvenient to only obtain the stimulating effect upon making or breaking the current. The far more efficient means of electrical excitation of nerve fibres is the interrupted current, and that not the directly interrupted current, but the induced form.

By this means a series of induction shocks are sent into the nerve at the rate of about 100 a second. The result is to produce a very easy and ready means of arousing nerve impulses.

Effects of Excitation on Nerve Fibres.

We have now to consider what happens in a nerve fibre when it has been excited by one or other of the means just described. The first question which we naturally ask ourselves is, What is its physical appearance under these circumstances? Does it exhibit any change in form or otherwise? The earlier observations of Rollett and others had shown that living protoplasm, when excited by electricity and other means, contracted or shrank; and Engelmann has shown that similarly the outlines of nerve fibres which have been irritated are uneven and undulating, as though their protoplasm had contracted. Nerve cells also have been stated to shrink when, in the living condition, chemical reagents have been applied to them (Fleischl), or when they have been stimulated for a considerable time (Hodge). These latter experiments, however, require considerable repetition before they can be fully accepted.

In pursuing our investigation of the direct effect

produced on the nerve fibre by its excitation we look, of course, for the physical changes which habitually accompany the exercise of functional activity on the part of living protoplasm. Those are: 1. Chemical changes; 2. Thermal changes; 3. Electrical changes.

1. *Chemical Changes.*

The chemistry of living protoplasm is so extremely vague at the present time, that it is not surprising to learn that at this moment we know nothing of the most delicate and complicated chemical changes in the whole body—namely, those in the nervous system. It has been stated (and contradicted) that nerve protoplasm behaves in this respect exactly like other protoplasm—that is to say, in its functional activity it tends to become acid and to yield the products of oxidation, but while at any rate on the latter point no doubt may reasonably exist, it certainly does as regards the former. Moreover, it is reasonable to suppose that the chemical changes which accompany the passage of nerve impulses along a mere conductor are probably so slight, that nothing but the most continuous exercise of the nerve channel would evoke alterations sufficient to be detected with our present relatively coarse method of experiment.

2. *Thermal Changes.*

The same is not quite true of the question of the development of heat; however, while we shall see later that this does accompany the activity of nerve *centres*, there is at present no evidence that any heat is developed in a nerve *fibre* during the passage of a nerve impulse along it. It is a familiar fact to you, and well illustrated by the experiment before you, that, when we cause an electrical current to pass along a wire, it heats that wire, owing to the resistance which the current meets with in its passage along the conductor. When a nerve is taken and stimulated at one end so as to cause a nerve impulse to travel along its fibres, no such heating of the protoplasm can be detected, although this question has received investigation quite recently, at the hands of Mr. Rolleston, by the most delicate method we know of. This method, which is well known to physicists, is that of laying the substance whose temperature is to be investigated, on a fine metallic conductor through which an electrical current is flowing, the circuit including a reflecting galvanometer, so that the slightest variation in it can be at once detected. Such a variation of the electrical current would inevitably follow the warming of the little testing conductor by as small an

amount of heat as $\frac{1}{1000}$ degree Cent.; yet, although the stimulated nerve was laid upon this conductor, no alteration was produced in the resistance; in other words, it was not heated even to so slight an extent as $\frac{1}{1000}$ of a degree Cent. It is possible of course, and perhaps we ought to say probable, that this method is relatively much too rough, and that by some instrument we may be able some day to demonstrate the rise in temperature, which, from *à priori* reasoning, it is very difficult to believe does not occur in nerve fibres when they are in a state of functional activity.*

3. *Electrical Changes.*

Of all the changes in nerve fibres that accompany the passage of nerve impulses along them, the electrical are at once the most important and the most easily demonstrated. But before I begin to speak of them, let me beg you clearly to understand that although we have evidence of an electrical change occurring simultaneously with the passage of the nerve impulse, that is not the impulse itself, any more than the effort, by means of which an engine-driver turns the lever which lets steam into the cylinder,

* See, however, Stewart: "Studies from the Physiological Laboratory of Owens College, Manchester, 1891."

is the force which starts the train in motion. The application of an electrical current to a nerve fibre, and which stimulates it, has nothing to do, save the indirect relation of cause and effect, with the electrical changes in nerve fibres when thus stimulated. It is true that the exciting electrical current enters the nerve locally where it is applied, and that its electrical energy passes *across* through the substance of the nerve from one electrode to the other ; but what passes *down* the nerve to reach the muscle is not that electrical current, but a nerve impulse or development of nerve energy, which is accompanied by its own electrical change equally to be evoked, as I have already said, by any other form of stimulus—*e.g.*, pinching, &c. What that nerve energy is, or how much it resembles electricity, or heat, or light, or magnetism, we have not the remotest idea. We know that any one of the forms of energy that we have just mentioned can be, to use popular language, converted into the other—as, for example, in the case I gave you just now, where the behaviour of an electrical current in a conductor is such that light and heat are produced ; but since we have no means of measuring or getting hold of nerve energy, we cannot tell what is the direct relationship between it and the electrical stimulus which calls it forth. All we can say, at the

present time, by way of putting the matter more clearly before our minds is, that the stimulating electrical current determines some molecular change in the nerve at the point where it happens to be applied, and that that molecular change we, for the sake of convenience, agree to call an excitatory change; and we further go on to say that that excitatory change is transmitted down the nerve fibre, and when it arrives at its destination it is, as in the case of a nerve-ending in muscle, transformed when it leaves the little motor nerve-ending and passing into the muscle, causes the mechanical change of form which we call contraction—*i.e.*, the kind of energy termed movement. I can now proceed, without fear of confusing my subject, to the electrical change which is developed in a nerve conductor or fibre when it is stimulated. Apparently, if a living tissue be absolutely uninjured and at rest, one part of it does not appear to be in a different electrical state to another part, but if it be injured the part which is damaged becomes, as we express it, electro-negative to the rest or uninjured portion of the tissue. This is indicated, as in Fig. 29, by the signs minus (–) and positive (+); the cut end of the isolated nerve is of course the injured part of the tissue, and we therefore find when we connect the cut end and the longitudinal surface

respectively with the galvanometer, that there is a distinct difference in the electrical state of the two parts of the nerve; that the electric potential is higher in the uninjured part than at the dying surface; and therefore if, as just stated, the two portions be connected to the galvanometer, that instrument reveals to us that, in popular language, there is a current flowing through it from the uninjured longitudinal surface to the cut transverse end.

This fact was not discovered until 1843 by du Bois Reymond, but, most remarkable and far-reaching as it is, it is of less importance from the physiological point of view, because, as we have seen just now, it really depends for its existence, or at any rate marked development, on an abnormal state of things—namely, an injury of the tissue. What, however, is of the most fundamental and far-reaching significance is the following, which was discovered also by du Bois Reymond—namely, that if a nerve impulse be caused to pass down such a nerve thus prepared, the passage of that nerve impulse along the fibres evokes in them a change in their electrical state of the following kind. The electrical difference between the uninjured and injured surfaces respectively undergoes a slight change, and owing to the fact of

its taking the form of a diminution in the previously existing difference, it is not improperly called a *negative variation.* Now, this negative variation is really the greatest discovery in the minute or intimate physiology of nerve structures of the present century; for if we are dealing with nerve fibres alone—*i.e.*, isolated—it is the only evidence we possess of the passage along such fibres of nerve impulses: consequently, when we are attempting to analyse the physiological activity of the spinal cord, when it is behaving as a conductor rather than as a nerve centre, we should without this method be ignorant in what that differentiation of function consists. This diminution of the previously existing electrical difference may be taken as indicating the development of an electrical current flowing in the opposite direction to the previous one, and therefore Hermann termed this negative variation, which is evoked by arousing the function of the nerve, the "action current."

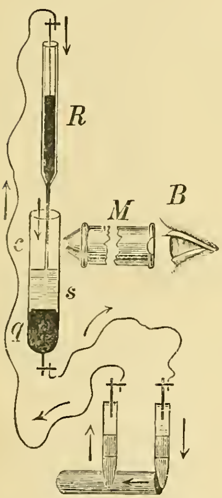
I shall speak of it under this title, not, however, that I think the term, strictly speaking, scientifically a good one, inasmuch as it rather tends to bind us to a particular interpretation of the phenomenon. Nevertheless, as it is the term which best connects this phenomenon with the passage of the nerve impulse,

it will doubtless commend itself to you, as being self-explanatory. This action current, fortunately, is developed even if we only send through a nerve fibre a single induction shock, the duration of which, as you know, is extremely short—less than a thousandth of a second: consequently, it is of still greater value to us as a means of knowing whether it is one big impulse alone which is passing down a nerve conductor, or whether it is a number of impulses with which we have to deal. Since, if it be the latter we could, provided we had a suitable instrument, see the successive development of a little series of action currents, one for each nerve impulse. This reasoning forms the basis of what is now spoken of as the galvanometric method of discovering the localisation, and indeed numerical estimation of nerve impulses; and it is the one which Mr. Gotch and I have employed in our researches.

I spoke just now of a suitable instrument for recording the existence of the action current: as a rule, this is effected by means of this beautiful galvanometer, named the Thomson reflecting galvanometer, after its inventor, Sir William Thomson. This instrument is so delicate that it is capable of appreciating the 30-millionth of an ampère; it is of course on this account extremely sensitive, and special precautions have to be taken in its use;

but these are well known, and can be discounted. It has, however, a serious disadvantage for our purpose, for while it shows, by a steady swing of the galvanometer needle, the existence of the action current, it is too slow in its swing to reveal a series of these if they follow each other pretty rapidly, inasmuch as the one succeeding the other at a very short interval, the needle has not time to swing back, and consequently they all become fused together into one large deflection. There is an instrument, however, which does move very sharply and quickly when even a weak electrical current is sent into it: this instrument is called Lippmann's capillary electrometer, and as made by Mr. Burch is extremely efficient; its structure is shown in this diagram (Fig. 34). It consists simply of a little capillary tube (*c*) containing mercury, which is immersed in sulphuric acid (*s*), and, when an electrical current is sent into it, the mercury advances along the little tube, and as quickly retreats when the current is shut off. But it also has a greater advantage—namely,

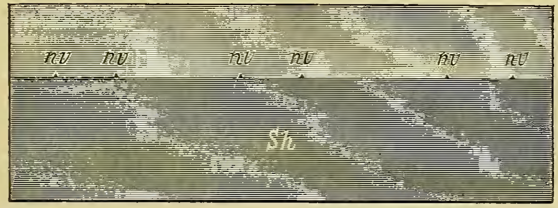
FIG. 34.



In this drawing the current in the nerve is shown as an action current.

that if we focus by means of the microscope (*M*) the image of this little capillary on to a slit with a very strong light, the electric light, and if we have moving behind that slit a sensitive photographic plate, we can take a photograph of the shadow cast by the mercury column; thus, if this be caused to

FIG. 35.



Drawing of a photograph. *Sh* is the shadow of the mercurial column. The little elevations *nv*, *nv*, are the little leaps the mercury makes when each single shock to the nerve induces an "action current."

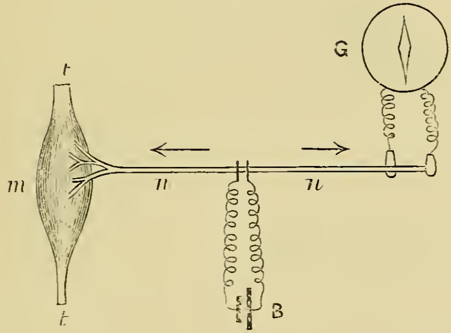
shoot up and down by the passage in and out of it of the action current, that shoot up and down will also be shown as a shadow on the photographic plate, and in this way we shall obtain an automatic record of the electrical effect produced in a nerve fibre by the passage of the nerve impulse. Such a photograph is shown in Fig. 35.

LECTURE VII.

WE have just seen that the single negative variation or diminution in the previous electrical state of nerve fibres is our only physical evidence, of a direct kind, as to what occurs in one when a single nerve impulse passes along it, but, although it is the only direct evidence at our disposal, it is of immense practical value, and this will be realised later when we see how it forms a reliable method for determining the paths of transmission in the central nervous system. Further, the extraordinary fact, of which I have spoken before, that nerve fibres conduct both ways when they are excited in the middle of their course, was also discovered by the use of this method. Thus, as indicated in the diagram (Fig. 36), excitation of the nerve (*n*) by the battery (B) causes the muscle (*m*) to contract, and at the same time the galvanometer (G) which is in connection with the other end reveals the presence of the "action current," or negative variation. From this it is evident that the nerve fibres have conducted upwards and

downwards in the directions of the arrows from the point excited. The other known fact concerning the transmission of nerve impulses along fibres is the rapidity of their passage, which is ascertained to be about 33 metres per second; in other words, about 100 feet per second. This is a rate which we can picture to ourselves readily enough, when we con-

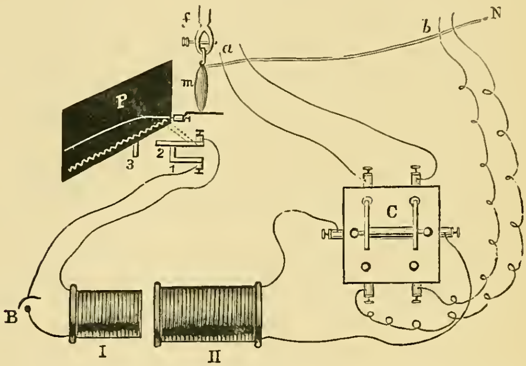
FIG. 36.



sider that it is just about equal to that of an express train going a trifle over sixty miles an hour. It has been directly measured by a very simple plan (Helmholtz) as follows: If we trace along the nerves from the spinal cord in the neck region down into the muscles of the upper limb, we find that they come near to the surface at different places. It is relatively easy for us therefore to stimulate the nerve for the small muscles of the hand, high up in the neck and low down in the forearm, as

shown in the diagram (Fig. 37) at *a* and *b* respectively. A suitable apparatus is then connected with the small muscles of the hand, and an electric signal, at the same time, with the exciting current. Finally, we have another electric signal marking the time.

FIG. 37.



Apparatus to record the moment at which a muscle contracts when a stimulus from an induction coil (I, II) is applied to different parts of the nerve (N), and so used to obtain evidence of the time taken for the passage of the impulse along the known length of nerve between *a* and *b*.

NOTE.—The above diagram represents a frog's nerve and muscle arranged for the experiment.

Now all these signals are made to write upon a blackened surface (*P*) which moves rapidly forward, impelled by a spring, and, in doing so, opening a key which allows the current from the battery to stimulate the nerve, and at the same time to record the fact of the stimulation on the plate. The apparatus,

attached to the small muscles of the hand being pressed upon by their contraction, similarly demonstrates the moment when that happens. Finally, marked below are the periods of time recorded. If now in the first place, when the nerve is stimulated high in the neck at *b*, we find that the total time expended between the moment of excitation and the contraction of the hand muscles is a certain amount which we may call (T); and if, further, we find the total time occupied between the excitation of the nerve at (a), and the corresponding muscular response, to be (t); then it is obvious that the difference between (T) and (t) must be the amount of time which is consumed in the passage of the impulse from *b* to *a*.

Probably all nerve fibres transmit impulses at the same rate; this position, however, has been strongly contested, and it has been stated that the impulses passing along the so-called afferent channels or sensory nerves travel quicker than the corresponding motor impulses; so too it has been suggested by Exner, that the rapidity of transmission of nerve impulses in the fibres situated in the nerve centres is different to that seen in the peripheral nerves, but of this there seems to be a considerable lack of evidence.

Mr. Gotch and myself have examined this point

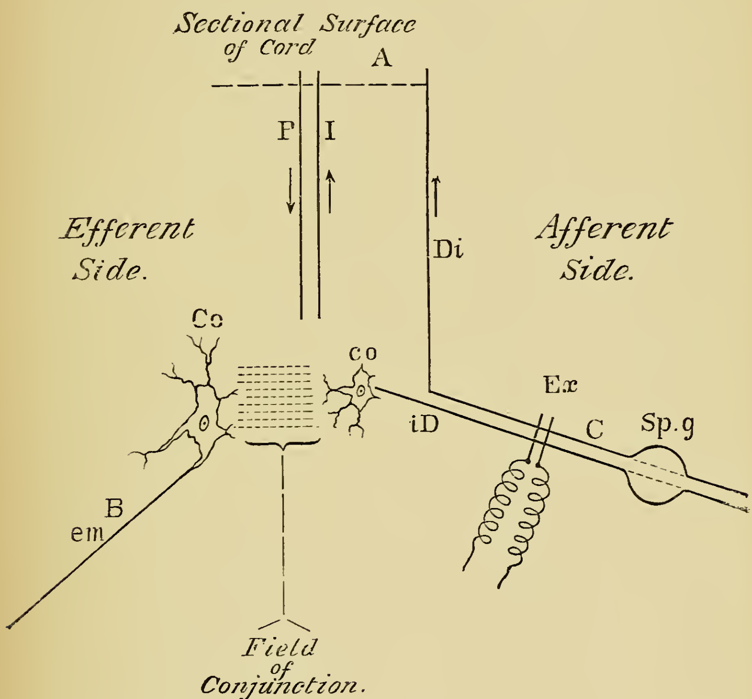
and have provisionally come to the conclusion that the fibres in the spinal cord conduct like those of the peripheral nerves. It may not at once be apparent why this rate of transmission of nerve impulses should be a matter of so much moment, but it will be obvious enough when we consider that if it were not for this determination of the rate in the peripheral nervous system we should be unable to determine the amount of time a nerve centre occupies in its work.

We will now begin the discussion of the leading principles which underlie the action of simple nerve centres, such as occur in the spinal cord, and will for this purpose give a description, in brief outline, of the structure of one of these. I believe we are justified in mentally building it up as consisting of three parts: (1) an afferent side for the reception of impressions, (2) a field of conjunction which connects the afferent side with (3) the efferent side from which impulses pass out down the nerves (see Fig. 38).

1. *The Afferent Side.*—Into the dorsal part of the spinal nerve centres enter the afferent channels from the posterior root. This part of the grey matter of the cord is called the posterior horn. For our present purpose it may be regarded simply as consisting of a complex maze of nerve fibres in which

are situated a number of small nerve corpuscles which are specially characterised by the tendency exhibited by their processes of breaking up into

FIG. 38.



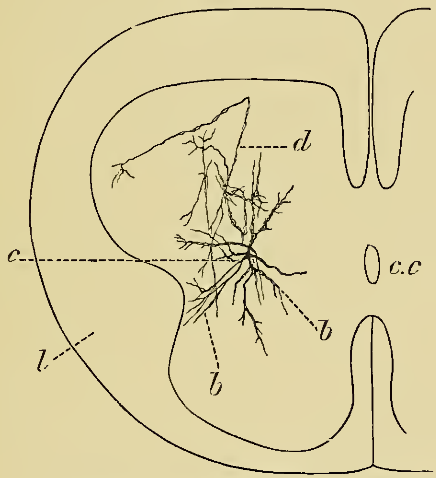
Sp.g = Ganglion on posterior root.
C = Posterior root.
Ex = Excitation electrodes applied to posterior root
iD = Indirect nerve sensory, *i.e.*, afferent path.
Di = Direct afferent path ascending cord in posterior column.
co = Small corpuscle of posterior part of grey matter.
I = Internuncial fibre.
P = Pyramidal tract, fibre from brain.
Co = Large corpuscle of anterior horn of grey matter
B = Anterior root.

finer and finer ramifications until these can be traced no further. The fibres of the afferent channels—*i.e.*, posterior roots have, it must be remembered, never been demonstrated to enter actually these small or posterior nerve corpuscles.

2. *The Efferent Side.*—We will pass at once to the consideration of the efferent side of the nerve centres because we do know something positive concerning it, as regards structure, whereas of the field of conjunction we know little or nothing. The efferent side of a nerve centre from which the impulses leave, consists of very definite anatomical structures—viz., large nerve corpuscles (see Fig. 41), the largest in the body, which give off numerous branches (see Fig. 39), the division of which is a matter of peculiar interest and importance. Before the method of staining, recently devised by Golgi, and by which he and, later, Kölliker, Ramon de Cajal, and others have discovered that the processes of these large cells have different destinations, it had been known since the time of Deiters, that there was one process in particular, which did not appear to branch, and which ran towards the anterior roots, and was apparently continuous with their fibres. We now know from a double method of staining introduced by Held and Flechsig, that this axis-cylinder process, as it

is called, does branch—*i.e.*, gives off, at right angles to the main course, one or two side "insulated" channels, and then enters the anterior root to issue as a motor or efferent nerve fibre.

FIG. 39.



Section of spinal cord.—*Kölliker.*

c = Large nerve corpuscle of grey matter of cord.
bb = Small branches with their non-communicating divisions.
d = Axis-cylinder process.
l = Lateral column.

3. *The Field of Conjunction.*—Of the Field of Conjunction in which the branches of the cells of the afferent and efferent sides respectively must meet, we know little or nothing. This is especially unfortunate, because it seems likely that this is the most interesting region of the nerve centre, and

that the obstruction to the passage of nerve impulses, which is obviously offered to such as may happen to attempt to pass through, is chiefly centred here.

The rapidly dividing branches of the nerve cells, both of the anterior and posterior cornua of grey matter, are directed towards each other, but they evidently do not meet, and the assumption is that they are lost in the ground substance of the spinal cord. Moreover, this is true also of nerve fibres which, whether coming by way of the posterior root, or as terminal branches of the pyramidal tract,* run apparently into the field of conjunction: they branch, and the ending of their branches cannot be traced, in fact no direct conjunction has ever yet been traced between the branches of the nerve cells, or those of the nerve fibre with the nerve cells. This absence of direct connection between the most important parts of the nerve centres is of course extremely difficult to understand, inasmuch, as it would seem that physical continuity of differentiated nerve protoplasm did not exist; but, as we do not know anything of the part which the ground substance of the tissue plays in its functional activity, we cannot make any surmise on the subject which would be worth mention. The fact is, of course, that

* Namely, the fibres which descend the spinal cord directly from the brain.

impulses do pass, and that in spite of obstruction or block, which we shall presently see is very marked under certain circumstances.

Turning now to the special physiology of nerve centres in the spinal cord, we find that apart from their regulating the changes in nutrition of the tissues to which they give fibres, they are principally charged with the duty of evoking muscular contraction or movement in response to received impressions from the outside. This movement does not only show itself by that of the large muscles of the limbs, but also of the circular fibres of the blood-vessels, in other words, by vaso-motor effects. The action of these centres is, however, easiest to study, when by their discharge they cause the large muscular movements; most therefore has been learned respecting their properties from this kind of effect, and it is consequently the one on which I shall lay the greatest stress.

(*a*) *Character of discharge.*—A spinal nerve centre differs in its mode of discharge according to the stimulus which evokes the disturbance of energy. In the first place, the centres will not react to a slight excitation; the first condition therefore is that the stimulus should be adequate—*i.e.*, have a certain force. The next point, which contains practically all that concerns the character of the discharge,

is that as to whether the stimulus is single or continued. If it be single and short the response is a single twitch, whereas if it be prolonged, a tetanus or continuous contraction can be evoked according to the state of activity of the centre. Further, the centre as a whole has, in the latter case, a remarkable power of adding up any inefficient stimulations that it may receive, and of giving out a muscular response to a sufficient repetition of these inadequate or subminimal stimuli.

So far I have spoken of the character of the discharge of the spinal centre, as it is revealed to us by the contraction of muscle as the consequence of the flow of nerve energy. But quite recently Mr. Gotch and I have proposed the employment of the electrical method for the elucidation of this point, and this can be done in the following manner:—

The electrical disturbance, which is set up in a nerve fibre during the passage of a nerve impulse along it, is, as I have already told you, termed the negative variation or action current. When you see it causing in the galvanometer the deflection of the needle, these deflections are easily recognised to have distinct characters; thus in a nerve *fibre*, when that is excited, the movement of the needle produced is a relatively quick or sharp response, and the

moment the stimulus is left off, the needle at once stops and quickly returns to its former place; whereas when we test the discharge of the nerve *centre* along the same fibre, we find that the deflection of the galvanometer has a different character. It is slower, and only gradually reaches to its maximum, and in the next place, when the current is shut off, it gradually returns to normal, contrasting in this respect very much with the effect observed in the fibre when that has been directly stimulated.

(*b*) *Amount of discharge.*—It would naturally occur to you, that what we should like to know is, what is the amount of nerve energy which is put out from a spinal nerve centre. Unfortunately, of course, as before said, we have no means of measuring amounts of nerve energy, physically speaking, and therefore we cannot say in positive terms what disturbance of energy there may be. But the electrical method here steps in and supplies us with a kind of comparative measurement, probably of intensities—*i.e.*, if we excite nerve fibres directly, for example, and obtain a certain amount of deflection, and if we then, on the other hand, cause a nerve *centre* to discharge down these same nerve fibres and obtain a different deflection, we shall probably not be far wrong in saying that the two readings are comparable together as indications of the intensity

of the nerve impulses in the two cases. We know also by this method that if it is not a question of intensities, the number of fibres concerned in the passage of the impulses must be very different, and that we have found to be true from our work on the spinal cord. There is always the possibility that both factors may be at work, and if we get a small figure as the result of a nerve centre's discharge into a mixed nerve—*i.e.*, a nerve containing both afferent and efferent fibres, or to use more popular language, sensory or motor respectively, it may mean that the centre is only discharging along a few fibres, efferent ones of course, or it may also mean that the intensity of discharge from the nerve centre is distinctly low. Reviewing the whole subject, there seems little doubt that, if the figure is very low in comparison with others, the intensity is probably affected. Now, as a matter of fact, it is a very low figure, for we find that the nerve, if excited directly, will give a deflection of 200 to 300 scale in the galvanometer, whereas the discharge of the nerve centre down the nerve fibre averages 26 only on the same scale, that is to say, about an eighth or a tenth of the amount. This is rather a revelation to us, because we now see that it may be possible in the future to find out some relation between the discharge from nerve

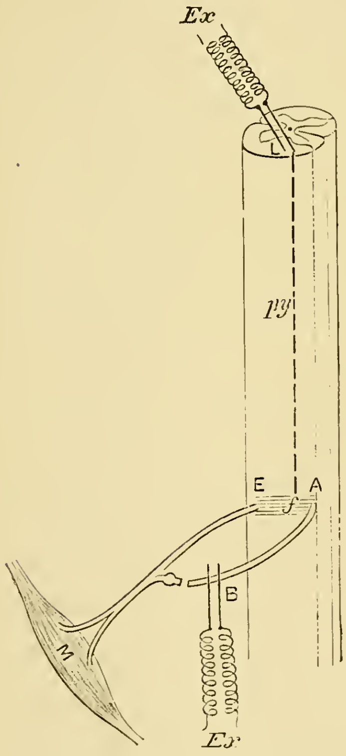
centres, and the amount of muscular force which is evoked, and in this way by some considerations allied to those upon which the conservation of energy is based, arrive indirectly at a rough physical conception of nerve energy itself.

(*c*) *Duration of the production of the discharge.* Perhaps the most interesting thing connected with the discharge of a nerve centre, if we could get it, would be the actual time taken up by the nerve cells in their work of converting the sensory or afferent impression into an efferent or motor impulse. This can be approximately arrived at in the following way:—

A nerve is chosen leading from a segment of the spinal cord, and a muscle in connection with it caused to pull a lever, which may break an electric current. If now any afferent nerves leading to that centre be stimulated by a single shock of electricity, the nerve centre will have the easy task of converting that single (exceedingly short) afferent impression into a motor impulse, and it does so, almost invariably producing a single muscular twitch: hence the single afferent excitatory state is converted into a single excitatory state on the efferent side by its passage through the nerve centre. The question therefore for us to decide, is how long a time is expended in that conversion in

the nerve centre. Now we must think what we are dealing with. In the first place, we are stimulating (Fig. 40), at a point say B, a sensory nerve fibre going up to a centre, and what we measure with our instrument is the whole length of time between the moment of throwing in the induction shock at B, and the commencement of the contraction of the muscle at M. If now we call the afferent or sensory side of the nerve centre A, and the efferent or motor cell of the centre E, then, from the whole time between the commencement of the impulse at B and its arrival at M, we must plainly subtract the time which is lost in going from B to A, and from E to M, and finally the time which is lost in the nerve-ending in the muscle itself (see Fig. 22). This last item has been ascertained by Helmholtz's method and found to be on the average

FIG. 40.



one-hundredth of a second, during which time, as it were, the motor nerve-ending is inducing the muscle to contract. The rate at which the impulses pass up to the centre and down from the centre we know already is 33 metres per second, therefore if we measure the length of the nerves we can easily estimate the fraction of a second that is lost during the passage of the impulse along them. Adding then these to the one-hundredth of a second lost in the nerve-ending, and subtracting from the total time expended from A to B, the answer comes out ·006 of a second. Some observers, it is true, find that the time is much longer than this, Exner, for example, says that the time is not six-thousandths of a second but six-hundredths. Such differences as these are not so serious as they appear, because you will naturally understand that nerve centres of all kinds are very delicate and very easily affected by the conditions surrounding them, such as temperature, nutrition—*i.e.*, the circulation, and the occurrence or not of previous excitation, and it is evident that the co-existence or absence of any of these factors must produce a varying activity of the centre and therefore a difference in the rapidity with which it works.

(*d*) *Automatism.*—I now enter upon a fresh

characteristic of the lowest nerve centres, including those which are to be found in the medulla oblongata or bulb and in the spinal cord. This is what is very frequently spoken of as automatism, and the usual example given is the action of respiration or breathing. Our breathing is effected of course by muscles which expand the chest and so draw air into the lungs, and then by others which, contracting again, expel it, so that the lungs are continuously being alternately ventilated. Now, the muscles are caused to contract for inspiration or breathing in, and for expiration or breathing out, by a regular and rhythmical discharge of nerve centres, at the rate of sixteen times per minute. Other instances of so-called automatism are the activities of centres all down the spinal cord, which have to do with the various organs of the body—have to keep up, in some cases, constant or tonic contraction where muscles are acting as valves, to hold back fluids, &c.; in other cases, to provide for alternate contractions and relaxations, and so forth. All these subordinate functions are carried on by these centres in a regular fashion, excited, no doubt, by impressions from the outside—*i.e.*, from the organs whose machinery they thus set in action; but at any rate, while the law of cause and effect is thus obeyed, a nerve centre is so far independent, that it discharges in a rhythmical

way and at a definite and characteristic rate, exercising, as it were, its own time of summation of impressions and its own period for their discharge. This automatism, as it is improperly called, of the lower centres is extremely interesting and important in many ways, because, understanding that the spinal centre can do this, it is easy for us to approach the next question which comes into close connection with the subject—namely, what happens in a spinal nerve centre after it has been excited. You have seen the graphic way of recording the muscular contractions which follow excitation of the nerve centre related to that muscle. Now, under certain circumstances, it is found, and has been graphically recorded, that the muscle, after it has responded directly to the excitation of the centre, at certain intervals following that excitation contracts again and again repeatedly. These contractions, small as they are, occurring after the primary effect or result of the excitation, are to be correctly spoken of as after effects, and they correspond unquestionably with the after effects, which next year we shall see are so very characteristic of discharge from the nerve centres in the cortex. It is plain from all this that the spinal nerve centres, especially when they have been to a certain degree disorganised by previous disease in the spinal cord, if they are excited

keep on discharging their energy, and stimulations, which were before disregarded by them, become quite enough now to effect this. A very striking example of this is what is termed, in clinical work, ankle clonus, where a sudden stretching of the leg muscles is sufficient to evoke a wonderfully rhythmical series of discharges of the spinal centres, causing a steady and rapid shaking of the foot, and this constitutes a very valuable sign in disease.

Intrinsic changes in the centre, in consequence of its functional activity.—As physicists, we would naturally desire next to know, just as in the case of the nerve fibres, whether any *chemical, thermal, or electrical* changes attend the development of nerve energy in a nerve centre, for theoretically it is impossible to conceive that it should take place without the concomitant exhibition of some alteration in one or other of these directions. In the case of nerve fibres, we saw that of chemical or thermal changes we had no evidence, but of course very marked electrical difference, which has proved so useful to neurologists. Of nerve centres we know still less, and as to whether or not their activity is accompanied by chemical alteration we are absolutely ignorant. Of heat variations in the spinal centres we are also quite ignorant; we shall see, when we come to consider the

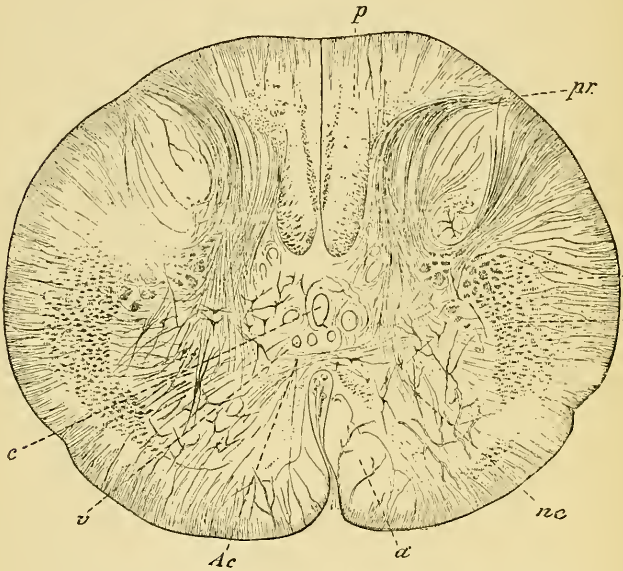
activity of the brain, that there heat-changes have been described, but none so far as regards the spinal cord. Now with respect to the electrical changes, that is still more a matter of doubt, because in the first place, as du Bois Reymond has pointed out, it is unlikely that we should have electrical differences exhibited in masses of nerve protoplasm in the shape of cells if those are quite uninjured, as they must be, naturally enough, for the performance of their functions. And moreover, quite apart from general considerations of this sort, the fact remains that every nerve centre is a combination of cells and fibres, therefore, if we connect such a centre with the galvanometer, as has been done in the case of the brain, we cannot say whether any electrical effects which we observe are due to the cells or to the fibres. In this state of ignorance therefore, we must leave this interesting topic.

Localisation of the origin of energy in a nerve centre.

The nerve cells in a spinal nerve centre on the afferent side are small, and, as we have already seen, branch and divide, and the terminations of such divisions are lost to sight in the cord. Yet we know that impulses spread from this region, through the in-

tervening field of conjunction, to the big nerve cells in the anterior part (Fig. 41) of the grey matter of the

Fig. 41.



Cross section of spinal cord of young animal.—*Kölliker*

p = Posterior column.
pr = Posterior root fibres entering cord.
c = Central canal.
v = Bloodvessel cut across.
ac = Anterior commissure.
nc = Large nerve cells of anterior horn of grey matter.
L = Lateral column.
tf = Fibres cut across—*i.e.*, running up and down the lateral column.

spinal cord, the elements of the efferent side of the nerve centre. Now comes the puzzling question, which of the elements of the centre is the source

of the nerve energy, is it the small cells of the posterior horn, is it the mysterious region which we have called the field of conjunction, or is it the large nerve cell which is so characteristic of the efferent region? Up to the present time these latter large corpuscles have always been called "motor," and, perhaps, by common comprehension of the meaning of that expression, they have obtained the reputation of being the source of the nerve energy; and it is a curious thing that although sensation stands to movement in the relation of cause to effect, nevertheless the afferent part of the nerve centre—*i.e.*, the sensation-receiving part, has not been credited with the function of which there is now good reason to believe it is the true source. For many years Dr. Bastian has taught that the origin of the nerve energy is to be looked for on this side of the nerve centre, and that, as a matter of fact, there is no direct evidence to show that the large anterior corpuscles are the sources of energy that they are supposed to be. But so far his observations have not been examined by the experimental method, and for that reason, perhaps, have not met with the attention that ought to have been accorded to them. Dr. Bastian showed, as long ago as 1869, that the fundamental process in every

movement is an æsthetic one, and that the sensory substratum of nerve action is the memory of former movements, by virtue of the impressions received from the moving parts. He therefore invented the term kinæsthesis, which very suitably expresses not only the memory of movement, but also the idea that this nerve action starts on the afferent or sensory side of the nerve centre. The experimental examination could not be performed clearly until the application of the electrical method, consequently the opinions I shall advance are as yet those founded only on the experiments of Mr. Gotch and myself. However, they were so clear and constant, that they leave in our minds no doubt of the truth of the proposition of Dr. Bastian which they so markedly emphasise. I must briefly summarise these facts, as time will not permit me to detail them at length. In the first place we found that the excitation of the spinal nerve centres was conveyed up the cord as a stream of nerve impulses in the posterior half of that organ and not in the ventral side: but much more striking evidence is to hand. To our surprise and, I must add, strongly against our preconceived notions, we discovered that the nerve energy of a discharging nerve centre overflowed down the posterior or afferent roots, as well as of course going down the ordinary efferent paths. This shed

at once a new light on the whole subject as to the source of energy in the nerve centres, because knowing, as we did from our other experiments, that impulses would pass up most easily the posterior side of the spinal cord and would only issue through the nerve centres in a very diminished degree, it was clear that the field of conjunction must afford a considerable block, and that therefore, if there was an overflow down the posterior roots, that overflow could only be reasonably surmised to come from a source of energy situated in the afferent side of the centre. It occurred to us to test this by a new way altogether, and that was to see whether nerve impulses would pass backwards through a nerve centre. This we effected very easily by simply applying our electrodes to the efferent or so-called motor channel—namely, the anterior root—and connecting the upper part of the spinal cord with the galvanometer so as to reveal the slightest amount of nerve impulses that might pass up the cord. We then discovered that nothing whatever passed up the spinal cord when we thus excited the anterior root.* The block therefore, that we spoke of just now, as existing in the field of conjunction must be of a very extreme character for anything

* This result was accurately foreshadowed by Prof. James in his remarkable work on "The Feeling of Effort," 1880.

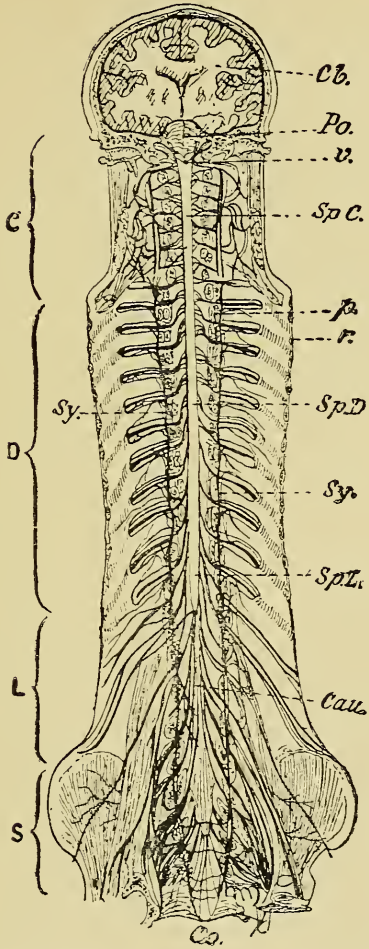
in the way of an impulse trying to pass backwards from the large nerve cells of the anterior horn. In this way you see we are brought logically back again to our original position—viz., that it is the afferent side of the nerve centre which is the source of nerve energy. I cannot do better now than conclude this general discussion of the behaviour of a simple nerve centre like that found in the spinal cord than by illustrating a simple reflex act. The commonest example, that one can think of, is the sudden withdrawal by us of our hand if we touch, or come in painful contact with, any object, or the involuntary closure of the eyelids when any object touches the eyelashes or the surface of the eye. In the lower animals, as is well known, the spinal nerve centres are so highly organised that, as in the tortoise or in the frog, the beheaded animal even is perfectly able to move its limbs in response to external stimulation. Until such external excitation is applied the limbs are motionless and flaccid, but the moment a stimulus is sent to the cord, by touching the foot for instance, the cord reacts by sending impulses to the muscles and the result is a movement of the leg that is irritated, that is to say of the one on the same side as the stimulation. Then if that be held so as to prevent its moving, the other leg begins to move and to thrust away the stimulating object. In other words, the impulse has spread across the cord from

the same or stimulated side to the opposite side. If we go further, and confine that leg also while continuing the stimulation, the fore leg on the same side as the stimulation will begin to move, and then after that the muscles innervated by the medulla oblongata or bulb, and later on, the fore leg of the opposite side. This remarkable arrangement of the activity of the nerve centres was discovered long ago by Pflüger and formulated by him in certain well-known Gesetze or Propositions. Thus, in the first place, he discovered that if an excitation passed up a sensory nerve it was first reflected, as we say, along a nerve fibre belonging to the same segment. Next, that if the fibre excited belonged to any part of the spinal cord the impulse would always tend to ascend and excite the centres in succession, as they lay higher than the points stimulated, until the bulb was reached, when the action stopped, or rather, the excitation being continued, spread over to the opposite side. Pflüger also discovered the interesting fact that when, on the contrary, any cranial nerve were stimulated, the excitation did not tend to pass upwards (*i.e.* forwards), but, on the contrary, downwards towards the bulb. This shows that the spinal nerve centres are gathered together more intimately for the passage of upward—*i.e.*, centripetal—impressions than for the converse.

LECTURE VIII.

I PROPOSE in this lecture to continue the consideration of the manner in which the nerve centres are built up together in the spinal cord, and the manner in which they are concentrated in the medulla oblongata, or bulb, at the upper end of the cord. For this we can conveniently start by again noticing that, for each piece of cord which lies opposite a vertebra, there are a pair of nerves, one nerve on each side (see Fig. 42). These nerves leave the spinal canal, which encloses the spinal cord, by the so-called intervertebral foramina, which are the little spaces between the arches of each of the vertebræ. These spinal nerves have therefore been enumerated and classified according to the vertebræ opposite which they lie, or rather by the vertebræ between which they issue. Owing to the fact that the skull as a segmented part of the body has become greatly altered in the process of evolution, it will be better to neglect the cranial nerves for the present. There are eight spaces to be provided for, as far as the

FIG. 42. (*Bourgery.*)



Cb = Cerebral hemisphere.
v = Medulla oblongata, or bulb.
SpD = Dorsal part of spinal cord.
SpL = Lumbar enlargement of spinal cord.
r = Rib cut across.
Sy = Sympathetic nerve.
D = Dorsal region of spine.
Po = Pons Varolii.
SpC = Cervical or neck enlargement of spinal cord.
cau = Cauda equina.
p = Pedicle of vertebra cut through.
C = Cervical region of spine.
L = Lumbar „ „
S = Sacral region of spine.

The nerves after they leave the cord are represented black.

cervical or neck region is concerned, hence we find that instead of seven cervical nerves (*i.e*, corresponding to the vertebræ) there are eight. In the dorsal region or back, the vertebræ, which carry the ribs, and which thus make up the chest, are spoken of as dorsal vertebræ, hence, each of the nerves which runs forwards between the ribs, and is therefore called an intercostal nerve, is at its origin a dorsal nerve. Then descending the spine we come to the lumbar vertebræ and sacral vertebræ, the nerves corresponding to which take their origin from the lumbar enlargement of the spinal cord and supply the abdomen, and also by joining themselves together into the great sciatic nerve, furnish the whole peripheral system for the lower limbs. The compact bundle into which the lowest nerve roots run down from the spinal cord is spoken of as the cauda equina, owing to its resemblance to a horse's tail. The nerves, however, when they leave the spinal canal, are combined together before giving off their branches to the limb and some of the trunk muscles, and these combinations are called plexuses.

We are now in a position to review the functions of all these spinal nerves, and we will complete our description of the centrés from which they take origin, seriatim, before we discuss the nerves and nerve centres which arise from the central apparatuses

in the medulla oblongata or bulb. In thus selecting, as it were, one part of the bulbo-spinal apparatus for consideration without regard to the other, we shall not be doing so much violence to the general plan of organization of the nervous system as might otherwise appear, inasmuch as although the character of the functions of the two parts is so very much alike, the divisions of the body and organs, which they supply, are so highly specialised in the case of the cranial nerves that they can very justly be placed in a separate division.

Kinds of Function to be provided for.

1. *Movement.*—Of all the various duties of the nerve centres in the spinal cord, which communicate with the body by the spinal nerves just described, the first and most important is that of movement. To make my description and classification of these centres, as regards the movements they regulate and produce, complete, it would be necessary for you to be thoroughly acquainted with the muscles, which are the real mechanical instruments employed for this purpose. This, however, in its entirety means an endless study, theoretically and practically, seeing that there are some three hundred muscles in the body. Fortunately, it is not

necessary to know them all, it suffices if we realise the sort of movements that have to be provided for. We must notice these a little closely, inasmuch as when we come, subsequently, to the localisation of function in the cortex of the brain, the nature of the movements therein localised is quite as much a matter of interest and importance as the particular part of the body moved. In other words, although we do not have to learn the exact position of each muscle, we must know the varying kinds of movements in general. Now the character of a movement depends on the nature of the joint which is in action, for if that, like the elbow joint, is a simple hinge, then the only movements that have to be provided for are flexion or bending, and extension or straightening. And on the other hand, if the joint is a ball and socket joint, like the hip, then obviously we shall have not only flexion and extension, but shall also find that the limb can be carried away from or towards the middle line of the body—*i.e.*, abducted or adducted, respectively; further, that it can be rotated in and out, or that it can be made to describe a circle—*i.e.*, circumducted. So much for the character of the movements of the different parts.

With reference now to the parts which themselves move, I may perhaps remind you that anatomically

we are in the habit of dividing the upper limb into the arm—*i.e.*, from the shoulder to the elbow, the fore arm, the wrist, the hand, the fingers, and the thumb, the first finger being spoken of as the index finger; similarly, with the lower limb we speak of the thigh between the hip and the knee, the leg from the knee to the ankle, the ankle, the foot and the toes, and the great toe is spoken of as the hallux. These different parts of the limb are each limited by joints, and are looked upon, therefore, properly as segments of it. In considering, therefore, the localisation of the centres which preside over the movements of the limbs, we must think of the latter as divided into these various segments, inasmuch as the localisation of the movements of each has been made out both in the spinal cord and in the brain.

As far as the spinal cord is concerned, its evolution is so closely wrapped up with that of the parts mentioned, that it is more convenient by far to divide these nerve centres according to the segments already detailed. The first investigators to throw light upon this subject were Professors Ferrier and Yeo, who discovered that, in the spinal cord of the monkey, the cervical and lumbar enlargements or swellings of the cord were respectively the seats of nerve centres for the different groups of muscles which moved the segments of the

limbs. They were followed in their work by others, especially Erb, Forgue, Beevor, &c., and the outcome of these observations, as well as the anatomical ones of Paterson and Herringham, has shown that the divisions of the spinal cord correspond with those of the limbs, in such a way that the uppermost divisions of the limbs have correspondingly the higher centres in the spinal cord, and the lower we go down the limb the lower are its centres in the spinal cord. A good example of this is to be found in the case of the upper limb, for the piece of the cord which contains the centres for it extends from the fifth cervical nerve to the first dorsal inclusive. Of the nerve centres in this piece, the highest—viz., those in connection with the fifth and sixth nerves—are the ones which regulate the movements of the shoulder joint, whereas the movements of the thumb are provided for by the eighth cervical and the first dorsal nerves. So too for the hip and great toe which are respectively provided for in the upper and lower parts of the lumbar enlargement. The arrangement of the centres for the character of movement is conditioned in pretty much the same way. As far as the upper limb, for example, is concerned, flexion is the rule in the upper half of the cervical region of representation; and extension or straightening is proportionally

marked in the lower part. Of course the nerve centres in the dorsal region of the spinal cord, as compared with those in the cervical and lumbar enlargements, are necessarily smaller and relatively insignificant, inasmuch as the muscles which they supply, being simply those for the movements of the ribs, are greatly limited in their actions.

2. *Sensation.*—The next important duty of the nerve centres in the spinal cord is to provide for the proper transmission and grouping together of sensory or afferent impulses. I am very particular to say afferent, because, as a matter of fact, whereas we find that if certain nerves are paralysed, there is in consequence loss of sensation to touch, to changes of temperature, and to pain, yet it would appear, from the researches of Goldscheider in particular, that these functions have a special channel—or, at any rate special nerve-endings in the skin. Whether they also have stations of their own in the spinal cord, wherein they are collected, arranged, and transferred to the brain, we do not know, but of course it would seem likely. We do know that, on the whole, if the limbs be divided into a front and outer half, and a posterior and inner half, that the sensation of these two halves is represented differently in the spinal cord, and that, for example, the sensory impulses of the front and outer parts of

the limbs travel to the upper parts of the enlargements for the respective nerve centres of the members.

One special form of sensation and its localisation in the spinal cord I particularly wish to allude to, while the representation of movement is fresh in our minds, because it also becomes of surpassing interest when we discuss the functions of the brain, I mean the afferent impressions, which we receive from the parts of our body which are in active movement,—*i.e.*, from the muscles contracting, from the tendons pulled upon, and from the joints which are pressed or stretched. These impressions collectively make up what is popularly called the muscular sense, and they form, as we shall subsequently see, the basis of every finely graduated movement; in this way they make up what we call practice and skilful dexterity. But what is of special interest as regards their development in the spinal cord is their employment in the muscular act of standing upright. When we lose our consciousness, as every one is well aware, we fall, we do so because our muscles are no longer actively superintended by the nerve centres of the spinal cord and the cerebellum (and probably, to a certain extent, of the cerebrum). The absence of the active contraction of the muscles causes the joints to relax, and hence

the body to collapse. Between this condition of total disorganisation and the normal condition, there is to be seen in disease every stage, and hence it follows that we may have only those particular fibres paralysed which are most especially connected with this important duty of preserving the proper relations between the impressions which are called the muscular sense, and the muscular contractions which secure the proper equilibrium of the joints. Under these circumstances, although the person does not fall, he nevertheless staggers, and the limbs are moved about in a very jerky and characteristically uncontrolled manner. This condition is spoken of as ataxy, and the disease which gives rise to it is called tabes. We shall see presently the paths of conduction of these impressions, and therefore we can postpone the further consideration of this matter, merely observing that it is not unlikely that what undoubtedly occurs in the lower animals, such for instance as in the frog, may partly also be present in man, and that the lower or bulbo-spinal centres may contain within themselves the proper organisation of both afferent and efferent parts for the harmonious production of some of our so-called complicated acts or movements.

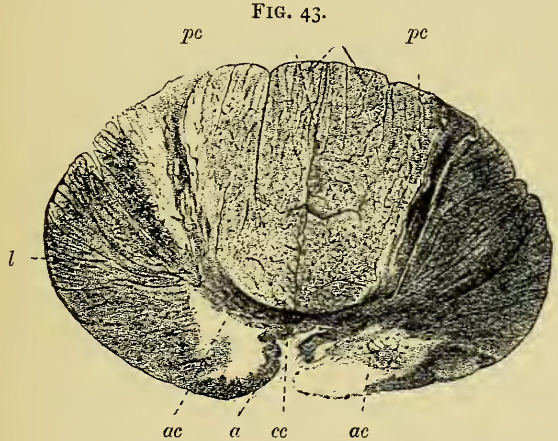
3. *Muscular Tone.*—There is a small matter or duty which is attended to and provided for by

all the spinal nerve centres which have to do with movement, and that is the preservation of muscular tone. I alluded to this before in speaking of the nervous system in the medusæ, and I showed you what was meant by tonic contraction, such as was first seen in the jelly-fish by Romanes. You will remember that the polypite of Sarsia underwent relaxation if the little nerve centres in the margin of the bell were removed. So it is with the muscles of all the higher animals, they relax if they no longer receive discharges from the nerve centres. It is hardly necessary to say that, since we cannot have an effect without a cause, these constant discharges of the nerve centres disappear under ordinary circumstances if the afferent channels leading to them are interrupted or destroyed. As Claude Bernard found, if the posterior or afferent roots were divided, all the muscles supplied by the particular centres of which the nerve roots had been cut became relaxed The same thing, of course, is produced in a very marked degree if the motor nerve to a muscle is similarly divided. We do not know the circumstances to meet which this constant, and, therefore, important physiological fact has been developed. Its existence is certainly conducive to quick and efficient contraction of the muscles, the functional

activity of which is enhanced by their tissue being a little stretched.

A striking example of the flaccidity of the muscles brought about by the destruction of the nerve centres is seen in a disease called infantile paralysis, which attacks young children, and in which the efferent part of the nerve centres, *ac*, seems unfortu-

FIG. 43.



nately to be picked out by the disease and destroyed, as you see in the accompanying figure (Fig. 43).

Under these circumstances the muscles of the paralysed limb are absolutely lax and the joints consequently become unfortunately distorted.

4. *Nerve Supply of Blood-vessels.*—The next duty of the spinal nerve centres, that must occupy our attention for a little time, is that of the remarkable apparatus, which forms the ground work

of the great experimental discovery made by Claude Bernard, which we are in the habit of speaking of as the vaso-motor system. The blood-vessels of the body (both arteries and veins) in their smaller branches are rarely of the same diameter many moments together. It has been shown by Wharton Jones and Lovèn that the vascular trunks or tubes undergo alternate contractions and expansions in a fairly rhythmical manner; further it was discovered by Bernard that in consequence of afferent impressions conducted to the spinal nerve centres, the arteries of a part may dilate, and that region consequently contain more blood than before, or, on the contrary, the vessels may contract and the part become pale and anæmic. The first of these latter phenomena is called vaso-dilatation and the second vaso-constriction. Each of the spinal nerve centres apparently possesses this property to a greater or less extent, but, as I pointed out to you, the fibres which concern themselves with the size of the blood-vessels leave the spinal cord—*i.e.*, the spinal nerve centres—by means of the dorsal nerves more especially, an arrangement which, as I have previously mentioned, seemed to be conditioned by, more than anything else, the greater importance of the vascular supply of the internal organs, inasmuch as the functions of the body

which are absolutely essential to life are by this means regulated and efficiently adjusted to its needs. To give you an idea of the remarkable power and influence of this system, I may mention that in some animals in which it seems to be well developed, and in whom the alimentary canal, for example, is of special importance, such for instance as in the rodents, if the nerves which run from the spinal centres for vaso-constriction are divided (and these are termed the splanchnic nerves) the result is to produce such an extreme and extensive dilatation of the vessels in the abdominal viscera that practically all the blood of the body collects therein, and the animal will die because not enough blood gets to the brain, lungs, and other important centres of life. In short, as has been appropriately said, in this case it is just as though the animal had died from loss of blood, though the blood had passed not out of the body, but merely into this particular system of blood-vessels.

The little centres, therefore, which preside over this function are dotted all down the spinal cord in each segmental division of it, the points at which they are especially connected being the beginning of the dorsal region, and the places where the first two or three lumbar nerves start from the lumbar enlargement.

5. *Secretion.*—The spinal nerve centres, like efferent centres elsewhere, when actively stimulated can determine the process of secretion by the glands of the body, thus revealing a further function which they subserve.

LECTURE IX.

WE come now to consider finally :

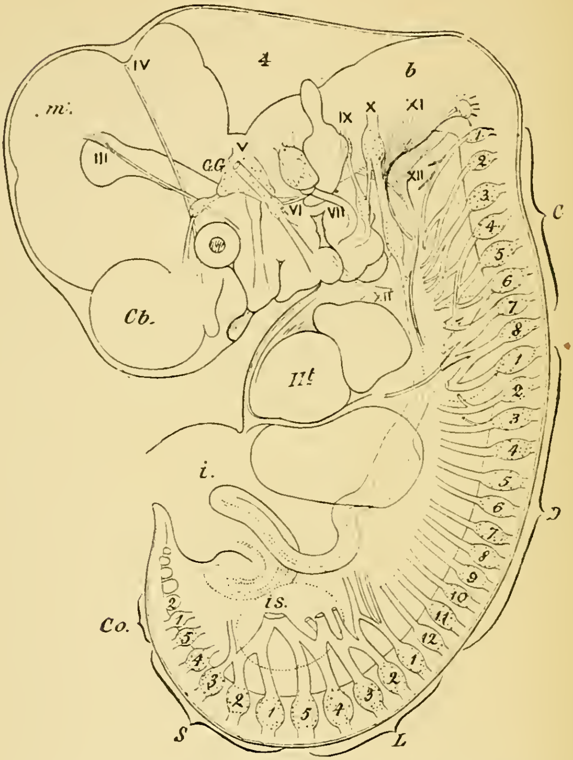
a. The arrangement of the foregoing centres in the Bulb or Medulla oblongata.

b. The arrangement of the conducting channels in the cord.

The arrangement of the centres in the bulb and the grey matter of what is called the mesencephalon is in no way peculiar. These centres, like those of the spinal cord, are simply stations for the reception and giving out respectively of afferent and efferent impulses, and the only point in which they differ from the spinal centres is that they are usually spoken of according to the number or name of the cranial nerve with which they are in relation. The names of these nerves partly interpret their function, and they are numbered in order from before backwards, as follows :—

1. Olfactory.
2. Optic.
3. Oculo-motor.

FIG. 44.



Human embryo.—*His*. Showing the peripheral nerves.

III to XII = The cranial nerves in order from the third to the twelfth.
Cb = Developing cerebral hemispheres.
m = Mid brain.
4 = Fourth ventricle.
b = Commencement of bulb, or medulla oblongata.
C (1 to 8) = The cervical nerves and ganglia on their posterior roots.
D (1 to 12) = The dorsal ,, ,, ,, ,,
L (1 to 5) = The lumbar ,, ,, ,, ,,
S (1 to 5) = The sacral ,, ,, ,, ,,
Co (1 to 2) = The coccygeal ,, ,, ,, ,,
Ht = Ventricle of heart.
i = Intestine.
is = Sciatic nerve cut at its origin.

4. Oculo-motor. Trochlear.
5. Trigeminal sensory and motor.
6. Oculo-motor.
7. Facial motor.
8. Auditory.
9. Glosso-pharyngeal.
10. Vagal.
11. Spinal accessory.
12. Hypoglossal.

All these nerves, in some measure or other, are comparable to the anterior or posterior roots of the spinal nerves, but what that relation is, is not yet known in its completeness.

The way in which these centres are grouped is also a little different from the spinal centres, inasmuch as they are placed relatively one to the other in groups and not merely in regular order one above another. This, as will be seen directly, is merely a convenience on account of the varied functions they have to subserve, and owing to the fact that some of them are in relation with even the most distant parts of the body. A good example of the way in which they are grouped and specialised is, I think, the centre of the oculo-motor nerves. This term oculo-motor is usually reserved only for the third nerve, but, as a matter of fact, the fourth and the sixth both supply muscles of the

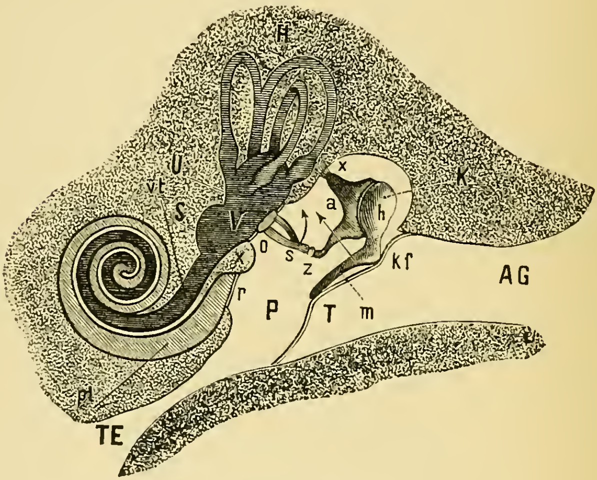
eyeball for moving that organ. From the experiments of Hensen and others on the lower animals, we know that there is not only a bulbo-spinal arrangement of centres for the movements of the eyes to direct the field of vision, but also an apparatus to control the movements of the pupil (which, as you know, is simply the hole in the iris, the little diaphragm in the eye which cuts off excessive rays), and at the same time a muscle, which, by contracting or relaxing, alters the shape of the lens, and focuses objects of near or far distance. This arrangement is called the mechanism of accommodation. The little centres which provide for the proper combined action of all these parts you see situated in the grey matter of what is called the aqueduct of Sylvius, but which is nothing more than a continuation of the central canal of the spinal cord. I have another reason for drawing your attention to this bulbo-spinal apparatus for the third nerve, since when we come to study the arrangements in the cortex cerebri for the movements of the eyes we shall see that the centres therein placed are relatively of great importance and extent.

Passing down the list of the cranial nerves and their centres we can leave out of count the fifth, because that is after all merely a combination of sensory and motor channels for the parts about the

jaws and tongue, and so also we need not dwell upon the centre for the facial nerve since that simply provides for the movements of the muscles of the face—*i.e.*, for respiration, mastication, &c. Coming to the next nerve, the eighth or auditory nerve, we do find here material for special interest. Not as far as mere hearing is concerned, since that naturally is only a variety of sensory or afferent impulses, but because of another and most important function which it has to perform. I have already spoken to you of the fact that the cerebellum or small brain is that part of the encephalon which chiefly regulates the movements of the muscles, so that we should stand upright and walk straight, when need be, without troubling our attention for the purpose. And further I have already suggested that the cerebellum gets the information it requires, as to the position of the various parts, from the contractions of muscles or, as they have been called, muscular sense impressions. This is not all however. It requires a more delicate apparatus than this for the appreciation of the position of the body in space. To effect this completely there is a special arrangement by means of which the cerebellum, through the agency of the eighth or auditory nerve, is kept informed of the position of the head. Now it is universally agreed that there are but three dimensions of space—*i.e.*,

length, breadth and height. Or, if we are to put it in other words for our present purpose, the estimation by the brain of its position in space will be provided

FIG. 45.



Vertical section (diagrammatic) of ear.

AG = External meatus, or channel of ear.
T = Drum. In section.
P = Middle ear of tympanum.
s, a, h = Ossicles—*i.e.*, little bones of ear.
V = Vestibule. From this branch upwards the three semicircular canals.

The spiral is the cochlea, for appreciation of tones. The auditory nerve is not shown, but pierces the bone at U to reach the bases of the semicircular canals and cochlea.

for, if the apparatus devised can tell when the head is being moved up and down, forwards and backwards, and from side to side. This is accomplished by an arrangement of three little canals, which from their

shape are called semicircular, and which are situated in connection with the ear, in the same bone, the ear bone. These little canals consist of a vertical one, a horizontal one and an obliquely directed one, as shown in the diagram, and they contain fluid, which is capable of irritating the ends of the auditory nerve by means of its movements according as the canal is tipped in any given direction.

A large part of the auditory nerve consequently forms the receiving organ of the impressions produced by the movement of the fluid according to the position of the head. It transmits those impressions to its centre in the medulla and thence to the cerebellum. When the fluid in these little canals is violently agitated, as in a sea voyage or in a swing or other ways, then the person feels giddy, the cerebellum becomes as it were bewildered and other symptoms appear, which are due to the excitation spreading in the bulb to the next centre—viz., that of the vagus.

The sense of taste is provided for by sundry other nerves—namely, the ninth nerve, or glosso-pharyngeal (the next to the auditory just described), together with a branch of the fifth nerve already mentioned, by means of which the hind part and the fore part of the tongue are respectively able to taste substances.

We come now to the study of the centres of the vagus nerve, and we may as well couple with it the upper part of the spinal accessory. This is by far the most important centre that we have to deal with, for the vagus nerve, as is shown in diagram (Fig. 28) supplies not only the lungs and the heart, but also the alimentary canal, and it is because it has all these diverse duties to perform, that it becomes the most influential nerve in the whole body, and as we shall see presently, destruction of its centre in the medulla oblongata is a fatal event. You will observe that I am speaking all along of the centres of origin of each of the cranial nerves, but when we come to regard those for the vagus, we discover that we are not yet quite able to say that such and such a path of it, or connections of nerve cells, are reserved for the function of respiration or for the regulation of the heart respectively. Therefore, it has long been the custom to speak of a respiratory centre and of a cardiac centre, &c. &c., using these terms to cover our want of exact knowledge as to which division of the structure it is to which we can refer the function about which we actually know more. I shall therefore adopt this older established nomenclature so as to make what I have to say harmonise with our exact knowledge and with customary terminology.

Respiratory Centre.

It is known from cases in which the upper part of the brain, even the cerebral hemispheres, remain undeveloped in certain instances in various animals, that nevertheless the individual, thus very incompletely built, can breathe and in other ways live. In other words it is obvious that the complicated bellows-like arrangement of expansion and contraction of the chest, to drive the air in and out of the lungs, must be regulated by the bulbo-spinal centres in the medulla oblongata and in the spinal cord. But it could only naturally be determined by direct experiment as to which part it was that had the required function. The experiments in question were designed and carried out in the most wonderful way, chiefly by the work of Legallois, and later Rosenthal. Rosenthal, by employing the method of dividing the bulb * at different levels, proved that therein was contained the central apparatus in question, that, if only it were intact, regular rhythmical impulses of the required rate of 14–16 a minute would pass out in order to effect the ventilation of the lungs. It then became naturally a very important thing to find out why this part of the bulb should perform this regular and most important rhythmical action, and

* Or medulla oblongata.

which further was the nerve tract along which the impulses came to and left the centre. Chiefly by Rosenthal's researches it was obvious that the vagus nerve was *par excellence*, the nerve of respiration. Numerous observations by various authors confirmed this view, and it was shown by Hering and Breuer that up the vagus nerve passed impulses from the lungs, according to the distention of those organs. Thus, when they were inflated with air, the respiratory centre, so called, received impressions which led it to give out impulses to the respiration muscles of an expiratory nature—*i.e.*, driving out the air from the distended lung: whereas these authors found, on the other hand, that if air were artificially sucked out of the lung, its consequent collapse caused the respiratory centre to make special inspiratory efforts. Similarly Dr. Semon has shown that the vagus nerve is the conductor of impulses from the lungs, of such nature that the centres in the medulla which move the vocal cords keep these latter apart as far as possible in quiet respiration, so that they should not obstruct the passage of air to and from the lungs. It will naturally occur to you that, as the respiratory muscles include the diaphragm, the intercostal muscles, which fill the spaces between all the ribs, &c., the spinal centres which innervate them must also be reckoned as integral

parts of the nerve respiratory apparatus. And this is doubtless true within certain limits. Thus, several authors, and most recently Wertheimer, have shown that if the spinal cord be divided just below the medulla oblongata, and if, to provide against the consequent total arrest of breathing, artificial respiration be applied and kept up, it is possible to so educate, as it were, the spinal nerve centres as to work them into a condition of keeping up respiratory movements. There seems to be, however, some reason to think that these movements under these circumstances are not exactly comparable to those evoked by the centre in the bulb.

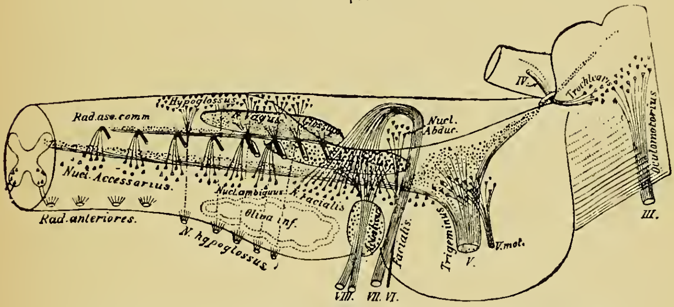
Cardiac Centre.

We are now compelled to pass on to the next fundamentally important centre—viz., that for the heart. Now when we consider the heart, we see at once that it does not require a special central apparatus to keep it going as the lungs do, since it contains within itself a well developed system of peripheral ganglionic nerve centres, and, in addition, its muscular substance in great measure is able to rhythmically contract under proper stimulation. The representation of the heart, therefore, in the bulb is more of the nature of a provision

for its proper co-operation with the other organs, especially the lungs, and since, furthermore, as an organ it is particularly susceptible to external impressions—*e.g.*, temperature, &c., and readily alters its rate thereby, it is of the first importance that there should be some nerve apparatus equal to the task of regulating its beats, and acting as a governor. That apparatus we are in the habit of speaking of as the cardio-inhibitory centre, inasmuch as it usually slows or stops the beating of the heart. This, we know (see p. 33) is provided by the vagus nerve, and when we turn to experiments, which have been made on the localisation of this centre in the medulla, we discover that it is situated at the lower end of the cavity of the fourth ventricle, the floor of which constitutes, as you know, part of the grey matter of the bulb, and, we may add, the principal part. The fourth ventricle, as I have explained before, is the expanded end of the central canal of the cord, and, being a lozenge-shaped area, it has a lowest angle in the middle line. This lowest angle, which is just where the central canal of the cord opens out on the surface, is, owing to its resemblance to the nib of a pen, called the calamus scriptorius. It is in the grey matter just above this calamus scriptorius that the cardio-inhibitory centre is seated. Stimulation of this spot with an electric current in an animal

will produce instant arrest of the heart as we saw when we stimulated the vagus nerve itself. But this part is also a portion of the region which serves the respiratory function, and underneath it pass many of the fibres which go down to the centres for the movements of the respiratory muscles low down in the spinal cord. It is not surprising, therefore, that Flourens termed this region of the bulb the

FIG. 46.



The medulla, or bulb, with the centres of the nerves arising from it.—*Edinger.*

"nœud vital," inasmuch as any sudden injury to this vital knot caused instant death, and this is no doubt due to the simultaneous arrest of the heart and of the respiration. To sum up, therefore, we see that there are a respiratory centre and a cardio-inhibitory centre in the bulb, that both are of the utmost importance, and that the latter certainly, and the former most probably corresponds with the centre of origin of the vagus nerve.

Vaso-motor Centre.

We now have to speak of a centre, which has most important duties, but the exact situation of which in the medulla oblongata we do not know. It has for its duty the maintenance of the calibre of the blood-vessels at a certain pitch. The heart, as you know, is nothing but a force pump continually injecting blood into a closed system of tubes, which we call the blood-vessels. Owing to its persistent action the blood, of course, is always at a certain pressure, hence when a blood-vessel is cut across the blood spurts out owing to the pressure with which it fills the vessels. That pressure, however, is not merely maintained by the heart, and it would be a very clumsy arrangement if it were, inasmuch as it would have to be continually accommodating itself to the needs of the body generally, and moreover could not provide for any sudden local demand for greater or less supply of blood to some limited part. This difficulty is got over by means of the vaso-motor centre. This was proved by the experiments made on animals by Owsjannikof, in which he, by the method of making sections and by stimulating the centre reflexly, proved that there was in the bulb a little collection of nerve cells, which were perfectly capable of causing a powerful contraction of all the

blood-vessels in the body if they were excited into activity, and, on the other hand, that if they became paralysed, then all the blood-vessels in the body dilated. I have already suggested to you that there were little centres for the same duty dotted all down the cord and that they were all governed by this one centre in the medulla oblongata; that was no doubt perfectly true, though the subordinate centres in the spinal cord are not, in man at any rate, or indeed in any of the higher animals, able to maintain such a perfect control of the vessels as is effected by the bulbar centre. I have only to add that the heart is directly connected with this centre by nerve fibres which influence the centre according to the amount of distention of the heart; hence if that organ is getting overpowered by blood the vaso-motor centre, in obedience to the information it receives from the heart, so loses its influence over the blood-vessels that they dilate and, the general blood pressure being thus lowered, the heart is relieved. This vaso-motor centre is obviously one of the greatest importance. We are unfortunately rather precluded as yet from a correct analysis of its duties, because the phenomena to which it gives rise resemble those produced by the heart itself.

Other Centres in the Bulb.

When we consider the manifold relations of the vagus nerve with the alimentary canal, it is obvious that the bulb or medulla oblongata must be the seat of various functions of different organs. Thus, the simple actions of the tongue and throat in swallowing are provided for by the nuclei of the vagus, spinal accessory and hypoglossal nerves, so that we are in the habit of speaking of the deglutition or swallowing centre. And so also the larynx is very widely connected with the same parts; and we have phonation on the one hand, and coughing on the other, all represented in the same region.

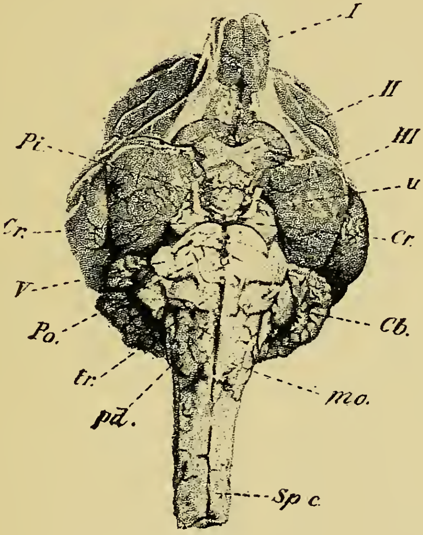
With this survey I am obliged to content myself at present, and must reserve further individual points after we have seen the functions of the cortex of the brain. I would only point out to you that, on the whole, the centres in the bulb resemble those in the spinal division of the lowermost or bulbo-spinal centres—viz., in being unilateral, each one of each pair is simply concerned with the same side of the body.

Before bringing this lecture to a conclusion one duty yet remains, and that is, to summarise and slightly extend the knowledge we have already obtained of the channels of conduction, which exist

in the bulb and spinal cord, and by means of which the impressions are conveyed to and from the brain.

The spinal cord is obviously a single mass of two

FIG. 47.



Base of cat's brain.

I = Olfactory bulb.
II = Optic nerves at their crossing or chiasma.
III = Third cranial nerve.
u = Hippocampal gyrus ending in unciform lobe.
Cr = Crus, or peduncle of brain.
Pi = Pituitary body.
V = Fifth cranial nerve.
Po = Pons Varolii.
tr = Trapezium.
pd = Pyramid.
Cb = Cerebellum.
mo = Medulla oblongata, or bulb.
Sp.c = Spinal cord.

defined halves. Following its plan beyond the bulb, we come first to the cerebellum, and we see that here each half has its own stalk running into it. So too the remainder of each half of the longitudinally directed fibres in the bulb soon diverge from those of the opposite side, so as to leave a wide space between them, and plunge into the base of each cerebral hemisphere. Where they leave the bulb proper, they are covered by transverse fibres, which connect the two halves of the cerebellum, and, owing to these fibres, this region was called by Varolius the "pons," or "bridge," and it is always known by this name, the pons Varolii (see *Po* in Fig. 47 of a cat's brain). Above the pons the divergent fibres form the cerebral peduncles, or crura cerebri, which parts, you must understand, are composed of afferent fibres going up to the brain and efferent fibres coming down from the brain. Of the former we know little; with the latter we are fairly familiar. Moreover, whereas the latter run straight down from the brain into the cord to join the bulbo-spinal centres, without suffering a break in their course, the former are interrupted in the bulb. We will therefore take the latter first, as easier of comprehension.

The Efferent Motor Channels.

These run on the ventral side of the crura, and are shown in the transverse section in Fig. 50, They then pass through the pons behind the fibres which connect the halves of the cerebellum, and so reach the bulb. When they get to the bulb, they are there gathered still more obviously into bundles, and then they perform the remarkable crossing that I referred to some lectures ago, and which, I also told you, was possibly due to the crossing of the optic nerve. This crossing of the pyramids, as the bundles of fibres are called, occurs just below the calamus scriptorius. A few of the fibres do not cross, but run down the same side of the cord in the anterior column, close to the middle line—*i.e.*, close to the anterior fissure. The vast majority however run down on the opposite side of the cord, and are spoken of as the crossed pyramidal tract. If they are injured in any part of their course, all the fibres below the point of injury degenerate, and by reason of this degeneration exhibit their situation in the spinal cord very clearly. These fibres terminate in the bulbo-spinal centres: that also I reminded you of when speaking of the delay or loss of time caused in the activity of these spinal nerve centres. Whether they join the network of the nerve cells,

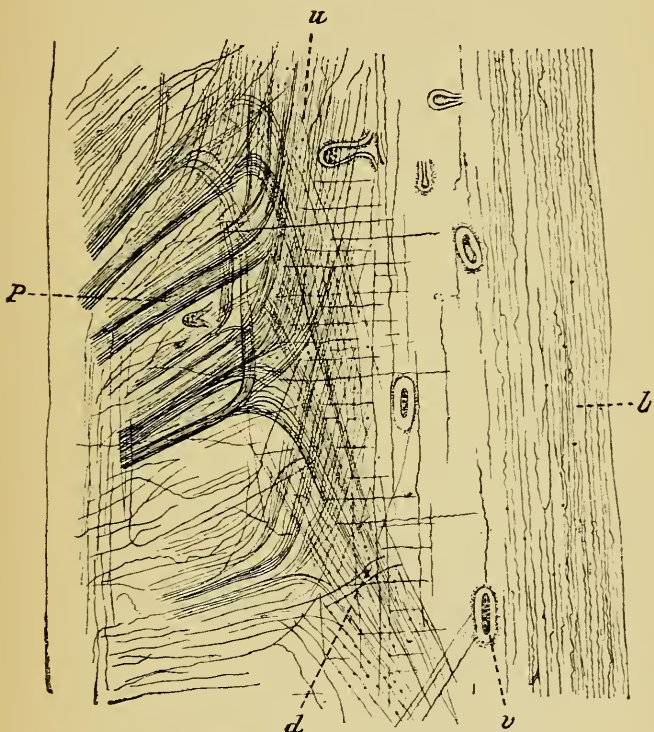
or whether they are lost in the field of conjunction, we do not know. All we know is, that they do not pass out directly into the fibres of the anterior root, hence we see that the centres in the cortex, of a necessity, discharge their impulses *via* the bulbo-spinal centres. Thus far matters are sufficiently simple.

The Afferent (Sensory) Channels.

On the afferent side our knowledge is less exact. The fibres of the posterior roots, which we know to enter the cord, as I have before explained to you, are divided into two great classes, first, those that run straight up the cord in the posterior column, without touching the nerve cells until they reach the medulla oblongata ; and secondly, those which are soon lost in connection with a nerve cell. Perhaps in all these, certainly in most, there is a preliminary division of the nerve fibre before it takes either of the above mentioned courses. And this division consists in its bifurcation (*p*) into two branches, one (*u*) which runs up the cord, and the other which runs down the cord (*d*), as shown in Figure 48. This much has partly been found out by the anatomical method of degeneration of the fibres, consequent

upon injury of the posterior roots, and also from the mode of staining nerve fibres introduced by Golgi.

FIG. 48.



Vertical section of spinal cord.—*Kölliker.*

v = Blood-vessel.

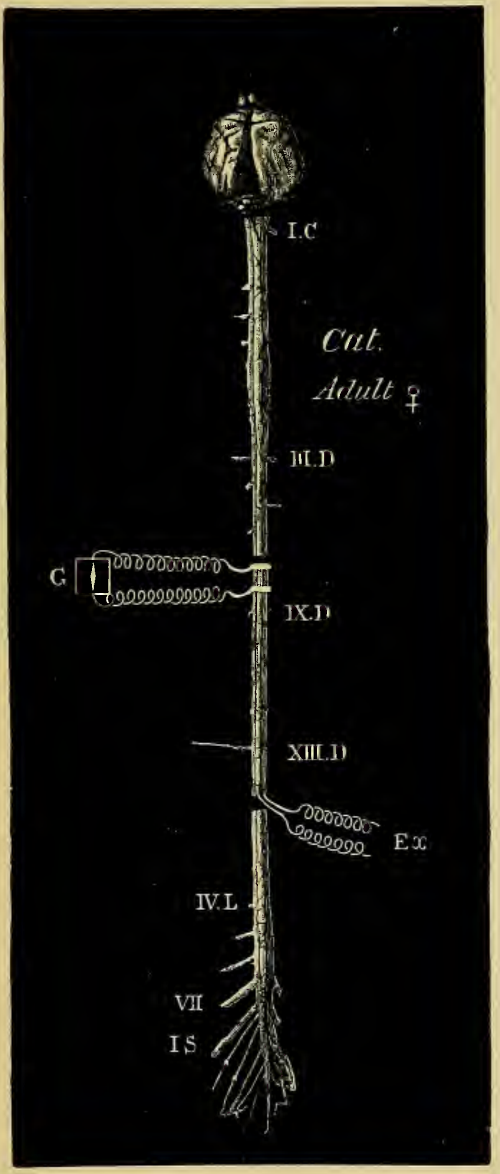
l = Fibres running longitudinally in the spinal cord.

The physiological plan of investigation however has also thrown light upon this difficult subject. But before examining it, we must first say that the direct

fibres just spoken of have not been traced further than the bulb, where they evidently terminate in nerve cells, from which, doubtless, nerve fibres pass up to the hemispheres along as yet unknown tracts.

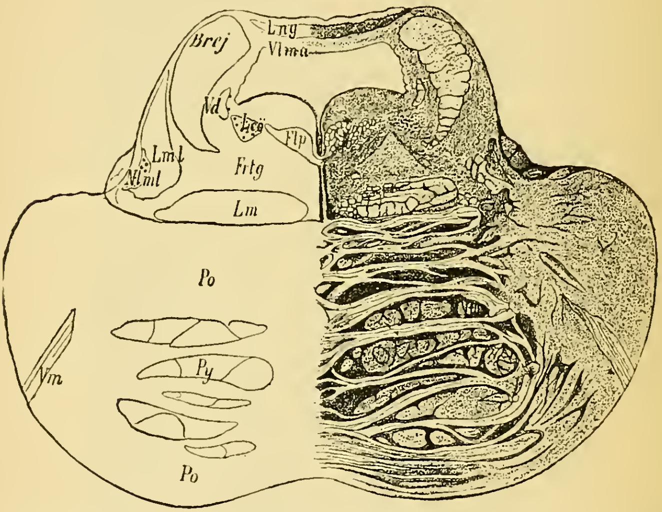
Turning now to the physiological method, we have already seen that these spinal centres, continually receiving afferent impressions, are also as continually sending them up the cord, by means of internuncial fibres connecting the centres with each other. Attempts have been made also to trace the conduction of impulses upwards by dividing the various columns of the cord in animals, and then seeing how far afferent impulses were blocked in their passage to the brain. Unfortunately this method is vitiated by one great fallacy—viz., the constant presence of activity on the part of the nerve centres, a factor which renders it impossible for a definite opinion, based upon this experiment alone, to be expressed as to the existence or non-existence of channels independent of nerve cells. Therefore Mr. Gotch and myself determined to investigate this subject by the electrical method. The arrangement of experiment is shown in Fig. 49; one part of the spinal cord was divided and connected with the galvanometer (G), and another part, above or below according to our wish, divided also, and each column of the cord respectively stimulated (*Ex*). The result naturally

FIG. 49.



was a deflection in the galvanometer, proportional to the number of fibres which were the seat of excitation. We have thus found that 80 per cent. of afferent impulses travel up the same side of the cord,

FIG. 50.



Transverse section of the mid brain through the pons Varolii.—*Obersteiner.*

Py = Pyramidal (descending) fibres cut across.
Po = Pons fibres running across from each lobe of cerebellum, &c.
lm = Fillet.
Frtg = Tegmentum.
Flp = Longitudinal fasciculus.

the 80 per cent. being made up of 60 per cent. of the total going up the posterior column, and 20 per cent. going up the lateral column: while of the remaining balance more than 15 per cent. passed up the posterior column on the opposite side and a trace up

the lateral column of that side. We know that in all probability, when these impulses reach the medulla oblongata, whether they come by the direct or by the indirect path, that they, after union with the nerve cells there situated, most probably gain the hemispheres by longitudinally directed fibres, which have received the name of the fillet and which pass deeply through the mesencephalon, through the peduncles and ventrally to the grey matter of the aqueduct of Sylvius; with this explanation we must remain satisfied. The impressions conveyed by these fibres or channels in the cortex of the brain are tactile, sensory impressions of heat or cold, pain, &c. &c., and of their final destination I shall speak in the next course of lectures.

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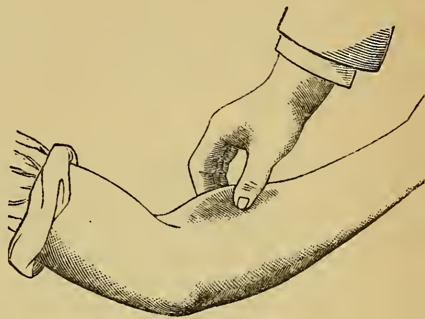

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